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UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

LANDSCAPE STRUCTURE IN A MANAGED FOREST MOSAIC OF THE SOUTHERN APPALACHIAN MOUNTAINS AND ITS INFLUENCE ON SONGBIRDS AND SMALL MAMMALS

A Dissertation

SUBMITTED TO THE GRADUATE FACULTY

in partial fullfillment of the requirements for the

degree of

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By

Peter Leimgruber
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LANDSCAPE STRUCTURE IN A MANAGED FOREST MOSAIC OF THE SOUTHERN APPALACHIAN MOUNTAINS AND ITS INFLUENCE ON SONGBIRDS AND SMALL MAMMALS

A Dissertation approved for the

DEPARTMENT OF ZOOLOGY

BY

Caryn C Vaughn

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Für Doris, Gerda und Eugen

PREFACE

This dissertation is presented as four chapters. Each chapter will be submitted to a refereed journal and is formatted accordingly. The first chapter has been submitted to *Ecological Applications*. The second chapter will be submitted to *The Wildlife Society Bulletin*, the third and the fourth to *Landscape Ecology*.

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ABSTRACT

Forests in the Appalachian Mountains of the eastern United States have been affected by human settlement and timber harvesting for more than two centuries and little old-growth is left. The remaining forests are extensive and heterogeneous mosaics with patches of different forest succession. A major concern for conservation in the Appalachian Mountains is how current management, such as logging, will alter these mosaics and their native faunas. Knowledge derived from studies on forest fragmentation and habitat loss may not apply to these landscapes because the current management does not fragment the forests, but changes the spatial configuration and relative importance of different forest successions. I studied the effects of management on the landscape structure and how these effects cascade through the ecosystem and influence small-mammals and birds.

Ecological research at the landscape scale requires techniques that have emerged in landscape and conservation ecology in the1970's: remote sensing and Geographic Information Systems (GIS). I utilized these techniques in combination with extensive field survey. My dissertation studies include research on how to improve current techniques for monitoring, such as landcover mapping, landscape analysis, and roadside monitoring of birds.

Roadside surveys are important tools for monitoring bird populations but may be flawed by habitat and edge biases. I used GIS and field surveys to determine these biases and test spatially explicit hypothesis about road effects on forest birds for the Warm Springs Ranger District of the George Washington National Forest in Virginia. Over 50% of the forest in the district was located within 500 m from roads. The distribution of forest habitats along roads was biased towards young forest-age classes and coniferous forest. However, differences in the presence of bird species with distance from roads were not related to the differential distribution of forest age-classes and forest types, but to distance per se. Edge-adapted species were most strongly correlated with distance from roads, indicating that roadside surveys are biased towards edge-adapted species.

Forest-managing agencies utilize large GIS databases that often have been acquired over areas much larger than the usual management units. Little is known about the accuracy and usefulness of this data. I compared accuracy and landscape patterns of the Little Mountain area in the Warm Springs Ranger District among three GIS maps: a landcover map of Little Mountain produced from satellite imagery, the Southern Appalachian Assessment (SAA), and the Continuous Inventory of Stand Condition (CISC). The maps differed mainly in the extent (area) that was mapped and this difference had a large effect on accuracy and landscape patterns. The landcover map of Little Mountain covered the smallest area (extent), was most accurate and -not surprisingly- displayed the highest heterogeneity in landscape patterns. The other maps (SAA and CISC) are of limited use for landscape studies and management because they underestimated rare landcover types, that occur in small and dispersed patches (i.e. mature forests and coniferous forests).

Because of the scale dependency of landscape-ecological relationships, I investigated how landscape structure changes with increasing spatial scales to determine thresholds where structure changes markedly. After establishing a baseline, I examined how logging affected the intensity and location of such thresholds. Using visual inspection and autocorrelation analysis, I found thresholds in landscape structure exist at 400-, 500-, and 800-m intervals from the outer edge of management units in my study region. While logging did not change threshold location and intensity for landscape indices that determine structure using all patch types (e.g. dominance, contagion, etc.), thresholds for mean patch size and percent cover for early-successional forest changed markedly. However, the changes in the landscape structure occurred at small spatial scales, but did not alter the structure of the entire forest mosaic. This may be explained by the high heterogeneity in the forest mosaics that was caused by previous, extensive logging.

Finally, I determined how logging affected small-mammal and bird communities at the local scale of the cut and the landscape scale of the forest mosaic. I divided the landscape into three zones based on distance from the cuts (zone 1, inside logged areas; zone 2, 20-400 m from logged areas; zone 3, 1,000-1,500 m from logged areas). Logging changed species presence and richness more drastically in close proximity of cuts than on the landscape and appeared to influence birds more strongly than mammals. The Acadian flycatcher (*Empidonax virescens*) and worm-eating warbler (*Helmitheros vermivorus*) disappeared from cuts, while the indigo bunting (*Passerina cyanea*) increased in presence. Generally, edge-adapted birds replaced forest interior species in cuts. Most differences in presence and richness of small-mammals were not due to logging in my study. I found landscape models that predicted changes in species presence for four bird species and one species of small mammals based on changes in landscape structure, mainly Shannon diversity and area of deciduous forest. While these models were significant, large amounts of variation remained unexplained. Differences in habitat characteristics may explain some of the remaining variation. However, I demonstrated that forest species are influenced by changes in the configuration and heterogeneity of the landscape mosaic.

Chapter 1

ROADSIDE SURVEYS: CHANGES IN FOREST COMPOSITION AND AVIAN COMMUNITIES WITH DISTANCE FROM ROADS

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Abstract. Roadside surveys are important tools for monitoring bird populations, but may not be accurate and/or representative because of habitat and edge effects associated with roads. We used a Geographic Information System and data from point counts to test spatially explicit hypotheses about habitat and edge biases in roadside surveys in the George Washington National Forest, Virginia. We determined the spatial distribution of forest age and type classes with distance from roads. In the summer of 1995, we monitored birds at 24 road points and 157 points at varying distances from roads. Mantel tests were used to evaluate whether presence, abundance, and diversity of avian species were affected by distance from road, forest type, and forest-age class. Over 50% of the forest was located within 500 m of roads. The distribution of forest habitats along roads was biased towards young forest-age classes. Coniferous forest was more common at close distances to roads than at far distances. However, differences in the presence of bird species between roadside points and interior points were not related to differences in forest distribution, but rather to distance from roads. While differences in presence of avian species and richness of edge-adapted species were significantly associated only with distance, differences in the richness of forest-interior birds were significantly associated with differences in forest age. There are biases in road surveys due to the edge properties of roadsides. Edge-adapted species are more strongly associated with roadsides than with specific forest types and forest-age classes. Forest-interior species are mostly influenced by the seral stage of forest habitats surrounding a survey point. While we found differences between roadside and interior bird communities, these differences can be accounted for and adjusted to produce unbiased estimates for population monitoring.

Key phrases: Roadside surveys for songbirds; forest composition with distance from roads; effects of distance from roads, forest age, and forest type on songbirds; edge-adapted songbirds affected by distance from roads; forest-interior songbirds associated with forest-age class.

Key words: forest roads; roadside surveys; forest composition; forest songbirds; avian communities; edge effects; Appalachians; Geographic Information Systems.

INTRODUCTION

Roadside surveys are an important tool for monitoring and assessing the conservation status of Neotropical migrant birds. Results from roadside surveys suggest population declines in these birds and have prompted a large number of studies on the possible causes (Askins et al. 1987, Robbins et al. 1989, Wilcove and Robinson 1990, Askins et al. 1991). These investigations are paralleled by research on whether roadside surveys are an appropriate technique for monitoring population trends in migratory birds (Bart et al. 1995, Hanowski and Niemi 1995, Hutto et al. 1995, Keller and Fuller 1995).

The Breeding Bird Survey (BBS), a roadside monitoring program, has provided extensive and consistent long-term data on bird populations (Sauer and Droege 1992). Its data have frequently been analyzed to assess the population status of Neotropical migrant birds (e.g., Robbins et al. 1989, Sauer and Droege 1992). However, roadside surveys may not be representative and accurate (Hanowski and Niemi 1995, Hutto et al. 1995, Keller and Fuller 1995). We investigated possible biases of roadside surveys caused by edge effects and habitat distribution.

Roadside surveys may be biased because the bird fauna associated with roads may not be representative of nonadjacent areas and habitats in the region (Bart et al. 1995). Differences in avian species composition and abundance between roadsides and nonadjacent areas can be caused by differences in habitat distribution with respect to roads, increased frequency of habitat disturbance along roads, and edge effects such as invasion of edge-adapted birds and increased nest predation (Schoenewald-Cox and Buechner 1992, Askins 1994, Bart et al. 1995).

Studies on road-count biases in forest birds indicate that edge effects result in increased species abundance and richness along roads as compared to forest interiors (Ferris 1979, Hutto et al. 1995, Keller and Fuller 1995). This increase is due primarily to the invasion by edge-adapted species (Hutto et al. 1995). However, differences in bird communities also could be attributed to differences in the distribution of forest types and seral stages with respect to roads. In a Colorado study, coniferous forest types and early seral stages covered significantly larger portions of the area along roads than expected based on their proportions in the total area (Miller et al. 1996). This is not surprising since in forested areas roads often are built to facilitate timber harvest. Thus, roadside counts may represent a selective sampling of habitat types and bird species in the landscape. While the habitat bias could be reduced by using stratified-random sampling procedures, biases caused by edge effects, such as increased competition and nest predation, are more difficult to take into account. The edge hypothesis and habitat hypothesis of roadside biases in bird counts need simultaneous assessment to better evaluate the efficacy of these techniques.

Spatially structured phenomena are difficult to quantify with the classical approach to statistical analyses in ecology (Legendre and Fortin 1989). Changes in habitat distribution, differences in severity of edge effects, and changes in composition of forest-bird communities with distance from roads are spatially autocorrelated, and observations cannot be assumed to be independent. Changes in forest bird communities with distance from roads may seem tied to edge effects, but in fact may be caused by a spatial gradient in habitat distribution. These interrelationships are commonly ignored

(Legendre and Fortin 1989, Rossi et al. 1992), but should be evaluated in spatially explicit analyses to determine the influence of forest roads on bird communities.

We investigated the distribution of habitat types with respect to roads and identified variables that may affect the composition, richness and abundance of forest birds in the southern Appalachian Mountains in eastern North America. The objective of our study was to test spatially explicit hypotheses about changes in forest composition and bird communities with distance from roads. Our three hypotheses were:

1. Different forest types and forest-age groups are not evenly distributed with respect to roads. We predict that forest age will increase with distance from roads. Mixed and coniferous forest types will occur at higher frequencies along roads because timber-harvest operations are likely to cause soil degradation in close proximity to roads (Norse et al. 1986).

2. Bird composition will change with distance from roads because of the spatial distribution of forest habitats caused by road construction and timber-harvest operations. We predict that early seral stages of forests associated with forest roads will result in higher frequencies of edge-adapted species in close proximity to roads. Species richness will be inflated close to roads because of the increased presence of edge-adapted species.

3. Edge effects produce changes in the bird communities with distance from the road. After removing statistical variation caused by forest vegetation, distance from roads will be negatively associated with edge-adapted species and positively associated with forest-interior species.

METHODS

Study area and survey points

Our study area is located in the George Washington National Forest in the Appalachian Mountains of Virginia. For investigations on the distribution of forest types with respect to roads, we used digital maps for 64,918 ha of the Warm Springs Ranger District (Fig. 1). Field studies on how distance from roads influences bird communities were restricted to Little Mountain in the Warm Springs Ranger District.

The study site for bird surveys on Little Mountain is approximately 8 km long and 4 km wide, comprising the west-facing slopes of the mountain with a range of elevation from 600–850 m. Within the site, 148 forest stands have been characterized with respect to age and vegetation. Ages of forest stands range from 1–180 years depending on the date of the last timber harvest. Older stands are dominated by red and white oak (*Quercus rubra* and *Q. alba*), while trees in younger stands are predominantly red maple (*Acer rubrum*). Other common tree species include chestnut oak (*Quercus prinus*), pignut hickory (*Carya glabra*), tulip poplar (*Liriodendron tulpifera*), Virginia white pine (*Pinus strobus*), and table mountain pine (*P. pungens*). Common understory shrubs are dogwood (*Cornus florida*) and mountain laurel (*Kalmia latifolia*).

GIS and landscape analyses

We analyzed digital maps in a Geographic Information System (GIS) to evaluate hypothesis 1 that forest habitats are not equally distributed spatially with respect to roads.

Digital maps for forests and roads were obtained from the U.S. Forest Service. All digital maps were ARC/INFO polygon and vector coverages. For analysis, we converted the polygon and vector maps into raster maps using the GRID module of ARC/INFO and specifying a 30-m cell size. The resulting grid coverages were used in all subsequent analyses.

The digital forest maps consisted of the Current Inventory of Stand Condition (CISC) and included information on forest age, forest type, dominant overstory trees, dominant understory trees, productivity, and management. We reduced these information classes and created two grid coverages: one delineating four forest-age classes (class 1, 1–50 years; class 2, 51–75 years; class 3, 76–100 years; class 4, >100 years); and one delineating three major forest types (type 1, coniferous; type 2, mixed coniferous-deciduous; type 3, deciduous; Fig. 2). For forest-age classes, we initially established classes for 1-25 years and 26-50 years, but later combined them into class 1 (1-50 years), because there were relatively few stands with an age of 26-50 years.

Using the road grid, we calculated a distance surface that gives the distance for each cell to its nearest road. We divided cells of the distance surface into 30 bands of 100-m width. The final band included all areas that were >3000 m from roads (Fig. 2).

Overlays using the distance-bands coverage with either the forest-age or forest-type coverage provided information on the forest composition at varying distances from roads. Within each band, we calculated total area and percent area for forest, for each forest-age class and for each forest type (Fig. 2). All GIS operations and analyses were performed using ARC/INFO and ARC/GRID for workstations. We used Mantel tests

(Mantel 1967, Schnell et al. 1985) to detect associations between distance from roads and differences in percent of forest types or forest-age classes.

Survey points and point counts

To test hypothesis 2 that bird composition changes with distance from roads, we conducted point counts on Little Mountain. We established 24 survey points on forest roads and 154 points at varying distances from roads. Survey points were separated by at least 250 m. For each survey point we determined the exact geographic position with Global Positioning Systems (GPS). We differentially corrected the GPS information with data from a nearby base station. After downloading the GPS data directly into a GIS, we determined the distances of the survey points to the nearest road.

We conducted two point counts at each survey point between 1 June and 1 July 1995. Each count lasted for 5 min and every bird seen or heard within 50 m of the study point was recorded. We visited each point once in the early morning between 0500 and 0730 h (Daylight Savings Time) and once between 0730 and 1000 h. Abundances were averaged over the two counts.

Statistical analyses

The search for spatial patterns in data, such as changes in forest composition and avian communities with distance from roads, implies that the observations are not independent because variables along spatial gradients are autocorrelated. Classical statistics often are not appropriate to evaluate spatial patterns, but an alternative technique–the Mantel test–can be useful for such analyses (Schnell et al. 1985, Legendre and Fortin 1989, Legendre and Vaudor 1991). Mantel (1967) developed a general method of matrix comparison to analyze spatial pattern in which two difference matrices are compared to test for significant associations between their elements. One of the matrices can include the geographic distances between the elements, while the other summarizes differences between elements in the character of interest. The computed Mantel statistic Z is the sum of the cross-products of the corresponding elements in the two difference matrices (Mantel 1967). We used the matrix correlation coefficient, r, which is calculated with standardized values from each difference matrix and by dividing the cross-product by $(n-1)$, where n is the number of pairs of matrix elements excluding diagonal elements (Smouse et al. 1986, Legendre and Vaudor 1991). The standardized statistics are equivalent to Pearson correlation coefficients and range between -1 and 1.

The significance of the statistic can be determined by performing a permutation test or by transforming the Mantel statistic r into a t-value of a normal distribution (Legendre and Vaudor 1991). The latter represents a good approximation if the number of elements in the matrices is large (Mantel 1967, Schnell et al. 1985, Legendre and Fortin 1989, Legendre and Vaudor 1991). We calculated the t-value to determine one-tailed probabilities for our Mantel tests because the number of matrix elements was large in all of our analyses.

We used Mantel tests to analyze differences in forest age and type with differences in the distance from roads. The geographic distance matrix in our study was determined as the distance in meters between all pairs of the 30 distance bands. Differences in percent area for forest age and type classes between all pairs of bands were calculated as average taxonomic distances (Legendre and Vaudor 1991, Rohlf 1993).

To test for significant patterns in distribution of selected bird species, we used Monte Carlo simulation, following procedures outlined by Pogue and Schnell (1994). The Monte Carlo simulation evaluated the degree to which the mean distance from roads at which a species was detected differed from the mean distance one would expect by chance alone.

We started with 178 survey sites and randomly drew (with replacement) the number of plots *j* at which individuals of species *k* were detected. Then we randomly drew the average abundance *a* for the species *k* from a pool that contained all average abundances that we detected at survey points for species *k*. We calculated a mean distance of the plots *j* from the road and used the random abundance value to weigh the mean distance. The resulting value was compared to the value calculated for individuals of each species *k* from the actual sample to determine whether the simulated value was less than the sample value or greater than/equal to it. The simulation was repeated 1000 times, and we calculated the two-tailed probability that the sample value deviated from chance expectation. Average deviation of the observed distance from the expected distance was calculated and used to score bird species for their sensitivity to roads. In these analyses, we included all species that were detected at a minimum of eight survey points.

To test for significant differences in species richness and composition of the birds relative to forest age, forest type, and distance from roads, we used analyses of variance (ANOVA). We grouped bird species into three categories: edge-adapted, forest-interior, and generalist species (Appendix A). Survey points were divided into six distance classes (0 [on road], 1–100, 101–200, 201–300, 301–400, 401–1000 m from a road) and the numbers of species, interior species, edge species were compared among the distance classes using an ANOVA. Similarly, we divided survey points into four forest-age classes (0–50, 51–75, 76–100, >100 years) and contrasted numbers of species, interior species, and edge species among classes using an ANOVA. Because the assumption that data points are independent may be violated by the existence of spatial gradients in the data, we repeated these analyses with Mantel and partial Mantel tests.

In the Mantel tests, survey points were split into two groups. Group 1 contained survey points located on or within 100 m of roads, while group 2 encompassed points at distances >100 m from roads. In this analysis, the Mantel test evaluated whether differences in bird abundance, presence-absence of species, species richness, edge-species richness, and interior-species richness were greater between the two groups than within. Because species richness and composition may be linked to distance from roads or some other gradient that varies in the same direction, such as forest age, it is difficult to differentiate between cause and effect. We used partial Mantel tests developed by Smouse et al. (1986) to calculate partial Mantel statistics between bird variables and forest-age class or forest-type class, by controlling for the effects caused by distance from roads (Legendre and Fortin 1989, Legendre and Vaudor 1991).

Forest age and type at each survey point were determined from the GIS.

Differences in forest age and type for all possible pairs of survey points were calculated as Euclidean distances (Legendre and Vaudor 1991) between their forest-age classes and forest types, respectively. For example, the difference in forest type between a survey point in deciduous forest (forest type 3) and a survey point in coniferous forest (forest type 1) was calculated as: 3 - 1 = 2.

We used raw data matrices of abundance and presence-absence for each bird species at each survey point. From the abundance matrix, we computed the average taxonomic distance between all pairs of survey points over all species. These distances range from 0 (when the same numbers of the same species are present at the two survey points) to large positive numbers (when the numbers of individual species vary greatly between the two survey points).

From the presence-absence matrix, we calculated the inverse of the Jaccard coefficient (Legendre and Vaudor 1991) between all pairs of survey points over all species. The resulting coefficient ranged from 0 (when the same species were present at the survey points) to 1 (when the two survey points shared no bird species).

Species richness, edge-species richness and interior-species richness were calculated for each survey, and the differences in these values between each pair of survey points were used in comparisons. For all computations involving Mantel tests, we used the R-Package developed by Legendre and Vaudor (1991).

RESULTS

Forest composition with distance from roads

Deciduous forest covered 76% of the forested area, while mixed deciduous-coniferous forest covered 19% and coniferous forest 5%. Forest-age class 3 was the most common seral stage, encompassing about 40% of the forested area, while age classes 1, 2 and 4 covered 10, 24, and 26%, respectively.

Because of the prevalence of roads in the region, most of the forested land was close to roads. While over 50% of the forest was located within 500 m of roads, only 2.5% was located at distances >2000 m (note top horizontal scale in Fig. 3).

Plots of total area and percentage area for each of the forest-age classes demonstrated that seral stages were not equally distributed with respect to roads (Fig. 4). While the total area covered by different forest-age classes declined with distance from roads, the percentage area declined most drastically for early-seral stages (0–50 and 51–75 years; Figs. 4a and c) and increased for forests that were over 100 years old (Fig. 4g). The difference among bands in percent area of forest-age classes was significantly associated with the difference among bands in distance from roads (Mantel test, $r = 0.67$, $t = 9.30$, $P < 0.001$). Bands that were close to roads and bands that were far from roads were more different in the percent area covered by different forest-age classes, than were bands that were close together. We detected a similar significant relationships that accounts for the spatial pattern in forest type ($r = 0.29$, $t = 4.06$, $P < 0.001$). The differences in the spatial distribution of forest types was mostly due to differences in the distribution of coniferous forests. While overall the area contained relatively little coniferous forest (5%), all of it was within 2200 m of a road.

Distribution of bird species with distance from road

We detected 50 species of birds during our surveys (Fig. 5). Eighteen species were never found at road points during surveys (Fig. 5). Most of these, with the exception of the Eastern Wood Pewee, White-breasted Nuthatch, and Mourning Dove, were observed at fewer than eight sites during the surveys. We did not detect Northern Flickers, Whip-poor-wills, American Crows, Chipping Sparrows, and Cedar Waxwings during surveys at road points, although we frequently encountered these species on roads before and after surveys. Many species of concern to conservationists, such as the Hooded Warbler, Louisiana Waterthrush, Kentucky Warbler, Cerulean Warbler, and American Redstart, had peak abundances at distances >300 m from roads.

Most species found at road points also were detected away from roads. If observations of a species were restricted almost entirely to roads, it usually was because the species was rare in the study area (e.g., Wood Thrush and Red-breasted Nuthatch).

To test whether a species was more frequently detected at closer or farther distances from roads than expected by chance, we used Monte Carlo procedures (Table 1). Deviations between mean detection distances and expected detection distances were significant for four species. Eastern Wood Pewees and Hooded Warblers were found at significantly greater distance from roads than would be expected by chance, and Indigo Buntings and Rufous-sided Towhees were at significantly shorter distances. Based on deviation scores, we ranked forest birds according to their sensitivity to disturbance by forest roads (Table 1). Species near the top of the table, such as the Eastern Wood Pewee, Hooded Warbler, and White-breasted Nuthatch, appear to be particularly sensitive to disturbance by roads. Species in the middle section, such as the Worm-eating Warbler, Ovenbird, Yellow-billed Cuckoo, Downy Woodpecker and Pine Warbler, seem to be little affected by roads. Species towards the bottom, such as the American Goldfinch, Tufted Titmouse, Indigo Bunting, Rufous-sided Towhee and Mourning Dove, tend to be associated with roads.

Differences in avian species composition between roads and forest interior

The numbers of species and of edge species were higher along roads than in the forest interior, but only the difference for edge species was statistically significant (ANOVA; Fig. 6). Because data collected along a spatial gradient may be autocorrelated, the significance for the increase of edge species with decreasing distance from roads may be overestimated. Mantel tests can identify such interrelationships in the data, while a partial Mantel test can be used to investigate the relative importance of variables that are autocorrelated. When survey points were divided into points 100 m from roads or less, and points at distances >100 m from roads, differences in percent area covered by forest-age classes were significantly greater between than within the two groups of points (Mantel test, $t = 1.63$, $P = 0.05$). As shown previously this is due to higher percentages for young forest close to roads and higher percentages for old forests away from roads (Fig. 4a, c, and g). However, we did not find a similar pattern for forest type among the groups of survey points (Mantel test, $t = -0.33$, $P = 0.372$).

Differences in presence-absence of species and edge-species richness between points close to roads and those away from roads were significant (Table 2). We did not detect any significant patterns in abundance, species richness, and interior species. Removing statistical variation caused by forest age and forest type using partial Mantel tests had little effect on *t*-values and did not change the significance of these results (Table 2).

We also found that differences in numbers of interior species were significantly associated with differences in percent area covered by forest-age classes when survey points were compared in the Mantel test (Table 3). Thus, survey points with different forest age compositions have different numbers of interior species present. Differences in presence-absence of species were significantly associated with differences in percent area covered by different forest types, reflecting the fact that survey points with different compositions of forest types are very different in avian-species composition (Table 3). Removing statistical variations caused by distance from road using partial Mantel tests did not alter these patterns. While we found spatial variation in forest-age classes and forest types when analyzed in distance bands for the entire ranger district, these patterns seemed to have little overall effect on the patterns we found in the avian community of our study area.

Based on these results, we reject hypothesis 2 that more edge species are found along roads because of the differential distribution of habitat types. The significant association between distance from roads and edge species does support hypothesis 3–that edge effects are the primary cause for the observed patterns.

DISCUSSION

Changes in forest composition

In forested regions of the eastern United States, road networks are dense and virtually all forests may be affected by roads. In our study, most of the forested land was in close proximity to roads. If edge effects on bird populations are assumed to extend up to 600 m into the forest interior from roads (Wilcove et al. 1986), then only 41% of the forest in the Warm Springs Ranger District remains unaffected. This is a conservative estimate because our study did not take into account habitat boundaries between agricultural lands and forest. In landscapes with such a prevalence of roads, off-road and on-road surveys may yield similar results simply because there is little unaffected habitat (Hutto et al. 1995). Thus, one may not be able to assess how far from roads is sufficient to prevent edge or habitat effects that change bird communities. However, our findings indicate that even in a disturbed forested landscape, changes in forest composition and bird communities with distance from roads will affect roadside surveys.

Our results demonstrate that the spatial patterns in forest age and type are strongly associated with distance from a road. Forest habitats surveyed during road counts are not a representative sample of forest habitats in the Warm Springs Ranger District (see Figs. 4a, c, e, and g). Compared to the entire forest district, habitats along roads are dominated by early- and mid-seral stages. The distribution of seral stages follows a spatial gradient with distance from road. This gradient is probably maintained by less frequent logging in areas that are less accessible. Where roads result in soil degradation and erosion, there also may be a gradient in forest types. In our study, coniferous-forest types, although relatively rare, tended to occur along roads.

Our findings are consistent with the results from other studies. Some landscape ecologists have even suggested that road density can be used as a measure of disturbance (Williams and Marcot 1991, Miller et al. 1996). Patch size of forest stands differed between forest areas with and without roads in the Kalamath National Forest (Williams and Marcot 1991). In Colorado, Miller et al. (1996) found that the percentages of early successional and coniferous forests was higher in a 20-m road buffer as compared to the surrounding forests.

Habitats along roads are subjected to change more frequently than habitats farther away. Timber cutting, as well as commercial and private development, are more likely to take place at close proximity to roads. Bart et al. (1995) pointed out that, because of higher disturbance frequency, avian population trends determined by roadside surveys may reflect local rather than regional trends. Our study demonstrates that logging is more frequent along roads and results in more early successional forest in these areas. The question of how this affects our ability to monitor population trends will require comparisons of long-term trends in bird populations along roads with trends in habitat conversion on local as well as regional scales.

Changes in avian communities

Previous studies usually have restricted comparisons between bird species detected during off-road and on-road surveys to analyses of abundances for individual bird species and of community measures such as species richness. Generally, results of such studies indicate that abundances of individual species and species richness are higher along roads as compared to forest interiors (Ferris 1979, Hanowski and Niemi 1995, Hutto et al. 1995, Keller and Fuller 1995). Typically, investigators have attributed the higher number of species alongside roads to the added presence of edge-adapted or shrubland species (Hanowski and Niemi 1995, Hutto et al. 1995, Keller and Fuller 1995). Distribution and abundance of forest-interior birds seemed little affected by forest roads (Hanowski and Niemi 1995). However, Keller and Fuller (1995) detected an increase in the number of rare species with distance from roads. Also, some species may be more sensitive to roads than others (Ferris 1979).

Our comparisons of the distributions of individual bird species with respect to roads (Fig. 5) and the results from our Monte Carlo simulations are in agreement with many of the conclusions from the previous studies. Some species show preferences in habitat selection with respect to distance from roads. In particular, forest-interior species are detected at greater distances from roads than expected by chance. Many of these species also show peak abundances in places considerably distant from roads (Fig. 5). As in the study by Keller and Fuller (1995), conducted in the Shenandoah National Park in Virginia, relatively rare species usually were observed at points far away from forest roads.

Our results from the comparison of the entire bird community emphasize the importance of edge effects. Significant differences in the presence-absence of species demonstrate that the species composition of birds along roads differ from that in the forest interior. This difference is caused by an increase in the number of edge-adapted species in close vicinity of roads. In our study area, forest age and type did not have an influence on presence-absence of species or the number of edge species. This suggests that differences in the composition of bird species are the result of an edge effect and not due to the spatial distribution of successional stages or forest types. Hutto et al. (1995) indicated that differences between off-road and on-road counts are best explained by multiple habitat factors, especially structural differences between roadside and forest-interior vegetation. Increased density of vegetation in narrow strips of vegetation along roads may account for increase in edge-adapted species. However, roads can influence the distribution of organisms in other ways that may explain the observed patterns. For example, roads may act as corridors along which edge-adapted competitors and predators can move into forest-interior habitats, decreasing the survival and nesting success of forest-interior species (Gates and Gysel 1978, Schoenewald-Cox and Buechner 1992, Askins 1994). Some of the effects of edge may extend up to 600 m into forest-interior habitats (Wilcove et al. 1986). Similar forest habitats at different distances from roads thus may have bird communities that differ substantially. We corroborated hypothesis 3 that observed patterns in the bird communities are primarily the result of edge effects.

The findings from our studies on the spatial distribution of forest-age classes and types demonstrated the importance of roads in structuring managed forests. However, the spatial distribution of forest age and type at the landscape scale of the entire district did not have a marked effect on the distribution of birds in our study area on Little Mountain. Interior-species richness was significantly associated with forest age, but this association was not affected by distance from a road. While some forest-interior species are sensitive to disturbance from roads, the number of interior species found at a survey point is little affected by forest roads, but depends largely on the age composition of the forest habitats surrounding a survey point. Also, the composition of avian species was not affected by distance from a road, but was most strongly influenced by differences in forest type between survey points.

Spatial patterns in avian communities

Cause and effect in spatially structured phenomena often are difficult to separate because the pattern may be caused by several interrelated processes (Sokal and Thomson 1987, Legendre and Fortin 1989). Also, several processes may result in the same spatial pattern (Sokal and Thomson 1987). While we conclude that edge effects are the reason for the spatial pattern in bird community structure, there may be alternative explanations.

Differences in species distribution between on- and off-road counts may be caused in part by other spatially structured environmental variables that were not measured. Roads are not placed at random in the landscape and topography is one variable that may exert a strong influence on where roads are build. Topography also can be responsible for gradients in climate, vegetation, and animal communities (McNab 1991). If roads are build to avoid obstruction by extreme topography, then on-road and off-road bird communities may be different simply because they occur at different elevations.

Edge effects, the influence of processes from adjacent habitats that extend along a spatial gradient into the interior of the other habitat (Forman 1995), are characterized by spatial dependence. Few studies on edge effects take this dependence into account, and research is needed using spatially explicit techniques to test for causal relationships.

Future roadside surveys

Although we found that data on avian communities collected along roads were biased towards edge-adapted species, there are several reasons why roadside surveys are important for the monitoring of songbird populations:

1. Few species were solely detected at large distances from roads in our and previous studies (Hutto et al. 1995).
2. Most of the public forests in the eastern United States include extensive road networks. In fact, there probably are few off-road areas that are not affected by roads.
3. When forest roads are narrow, results from off-road and on-road counts have been found to be very similar (Hutto et al. 1995).
4. Biases caused by differences in habitat distribution with distance from roads can be overcome by stratified-random sampling procedures.
5. Spatial gradients are not restricted to roadsides and may cause other biases (caused by elevation, climate, etc.) in data collected from off-road transects.
6. Roadside points easily can be located in consecutive years, while off-road points may be "lost". Thus, using on-road surveys may improve consistency.

We find that roadside surveys are a valid and important technique for the monitoring of bird populations. Breeding Bird Surveys provide the only long-term data on bird populations collected at large regional scales. The need for such data is reflected by the large number of publications that take advantage of this database to study population trends in birds (e.g., Robbins et al. 1989, James et al. 1992, O'Connor 1992, Sauer and Droege 1992, Witham and Hunter 1992). However, it is important to investigate and analyze the limitations of such data sets. Previous authors have made suggestions how roadside surveys in forest habitats could be improved. Stratified-random sampling based on data about habitat distribution of the region will account for potential biases in habitat distribution along roads (Hutto et al. 1995). Smaller roads should be included in surveys because they are more similar to off-road habitats (Hutto et al. 1995). Bird monitoring should be habitat specific (Hanowski and Niemi 1995). Habitats that do not occur along roads should be sampled with off-road surveys. For long-term monitoring, it will also be useful to assess and document habitat change along roads. Finally, statistical procedures should be used to describe and quantify spatial patterns in the data. Ecologists and conservation biologists need to acknowledge and consider the spatial nature of the phenomena they study.

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APPENDIX

Common and scientific name for species and their classification as edge (E), generalist (G), and interior (I) species.

Common name	Scientific name	Type
Ruffed Grouse	*Bonasa umbellus*	G
Wild Turkey	*Meleagris gallopavo*	G
Mourning Dove	*Zenaida macroura*	E
Whip-poor-will	*Caprimulgus vociferus*	G
Yellow-billed Cuckoo	*Coccyzus americanus*	G
Ruby-throated Hummingbird	*Archilochus colubris*	E
Red-bellied Woodpecker	*Melanerpes carolinus*	G
Downy Woodpecker	*Picoides pubescens*	G
Hairy Woodpecker	*P. villosus*	I
Northern Flicker	*Colaptes auratus*	G
Pileated Woodpecker	*Dryocopus pileatus*	I
Eastern Wood-Pewee	*Contopus virens*	G
Acadian Flycatcher	*Empidonax virescens*	I
Eastern Phoebe	*Sayornis phoebe*	G
Great Crested Flycatcher	*Myiarchus crinitus*	G
Blue Jay	*Cyanocitta cristata*	G
American Crow	*Corvus brachyrhynchos*	E
Black-capped Chickadee	*Parus atricapillus*	G
Carolina Chickadee	*P. carolinensis*	G
Tufted Titmouse	*P. bicolor*	G
Red-breasted Nuthatch	*Sitta canadensis*	I
White-breasted Nuthatch	*S. carolinensis*	I
Blue-gray Gnatcatcher	*Polioptila caerulea*	G
Wood Thrush	*Hylocichla mustelina*	G
American Robin	*Turdus migratorius*	E
Gray Catbird	*Dumetella carolinensis*	G
Cedar Waxwing	*Bombycilla cedrorum*	E
Yellow-throated Vireo	*Vireo flavifrons*	G
Solitary Vireo	*V. solitarius*	G
Red-eyed Vireo	*V. olivaceus*	G
Northern Parula	*Parula americana*	G
Prairie Warbler	*Dendroica discolor*	E
Pine Warbler	*D. pinus*	I

APPENDIX. Continued.

Common name	Scientific name	Type
Cerulean Warbler	*D. cerulea*	I
Black-and-white Warbler	*Mniotilta varia*	I
Yellow-breasted Chat	*Icteria virens*	G
American Redstart	*Setophaga ruticilla*	E
Worm-eating Warbler	*Helmintheros vermivorus*	I
Ovenbird	*Seiurus aurocapillus*	I
Indigo Bunting	*Passerina cyanea*	E
Rufous-sided Towhee	*Pipilo erythropthalmus*	G
Chipping Sparrow	*Spizella passerina*	E
Brown-headed Cowbird	*Molothrus ater*	E
American Goldfinch	*Carduelis tristis*	E

TABLE 1. Comparison between mean detection distance and expected detection distance for forest birds using a Monte Carlo procedure with 1000 simulations. Distances in meters and weighted by average abundance of birds at survey points.

		Mean distance (m)		
Species	Sites	Observed	Expected	Deviation
Eastern Wood Pewee	9	388	199	188*
Hooded Warbler	10	343	202	145*
White-breasted Nuthatch	9	309	202	107
Black-capped Chickadee	15	283	202	82
Blue Jay	9	277	202	26
Brown-headed Cowbird	19	268	198	69
Solitary Vireo	9	235	201	34
Acadian Flycatcher	24	227	198	28
Pileated Woodpecker	19	225	201	25
Worm-eating Warbler	89	216	199	18
Ovenbird	35	202	200	3
Yellow-billed Cuckoo	18	201	199	2
Downy Woodpecker	16	194	200	-5
Pine Warbler	27	188	196	-9
Red-eyed Vireo	92	187	199	-12
Blue-gray Gnatcatcher	27	185	199	-14
Scarlet Tanager	63	184	198	-15

TABLE 1. Continued

		Mean distance (m)		
Species	Sites	Observed	Expected	Deviation
Black-and-white Warbler	20	182	199	-19
Great Crested Flycatcher	13	178	201	-23
American Goldfinch	48	173	199	-26
Tufted Titmouse	27	157	201	-44
Indigo Bunting	83	151	199	-49**
Rufous-sided Towhee	28	134	201	-67*
Mourning Dove	8	134	201	-67

* $P < 0.05$; ** $P < 0.01$

TABLE 2. Results (*t*) of Mantel and partial Mantel tests for differences in bird communities between groups[†] relative to within groups of survey points. Survey points divided into two groups based on location relative to roads. Partial Mantel tests used to control for effects of differences in percent area for forest age and for forest type.

		Partial Mantel test controlling for differences in	
Variable	Groups	Forest age	Forest type
Abundance	1.32	1.28	1.36
Presence-absence	4.16***	4.15***	4.16***
Species richness	-0.95	-0.97	-0.96
Edge-species richness	2.59**	2.58**	2.60**
Interior-species richness	0.67	0.61	0.68

[†] Group 1 consists of all survey points located within 100 m of roads and group 2 includes all other survey points.

* $P < 0.05$; ** $P < 0.01$; ***, $P < 0.001$

TABLE 3. Results (*t*) of Mantel tests for associations between differences in bird communities and differences in percent area covered by forest-age classes and forest types, respectively.

Variable	Forest age	Forest type
Abundance	0.46	1.71*
Presence-absence	0.40	-0.33
Species richness	0.50	-0.69
Edge-species richness	0.65	0.33
Interior-species richness	2.69**	1.13

* $P < 0.05$; ** $P < 0.01$

FIG. 1. Forest cover in Warm Springs Ranger District of George Washington National Forest in Virginia (digital data courtesy of U.S. Forest Service of George Washington National Forest).

FIG. 2. Processing steps and digital data in analyses of forest age and type distribution with respect to roads. Forest data from Current Inventory of Stand Condition (CISC).

FIG. 3. Total and cumulative percent forest area with distance from a road.

FIG. 4. Percent and total area of forest-age classes with distance from a road.

FIG. 5. Abundances of bird species relative to distance from a road. Abundances were ranged for each species between its minimum (set at 0) and maximum (set at 1). Species marked with an asterisk were used in statistical analyses (see Table 1).

FIG. 6. Species richness relative to distance from road for (a) all species, (b) interior species, and (c) edge species. Significance levels given for one-way ANOVAs. Whiskers indicate standard errors.

Fig. 1

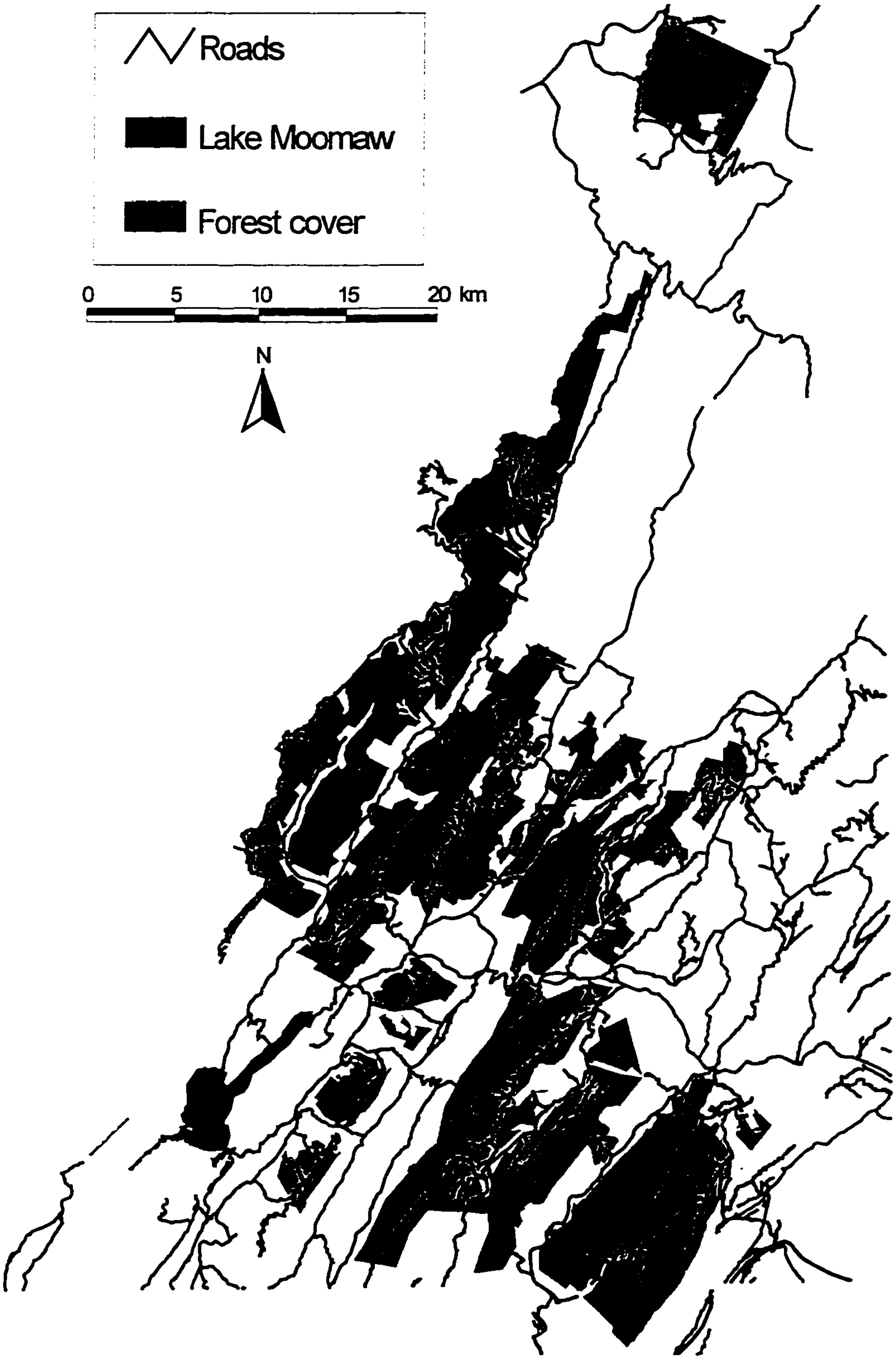
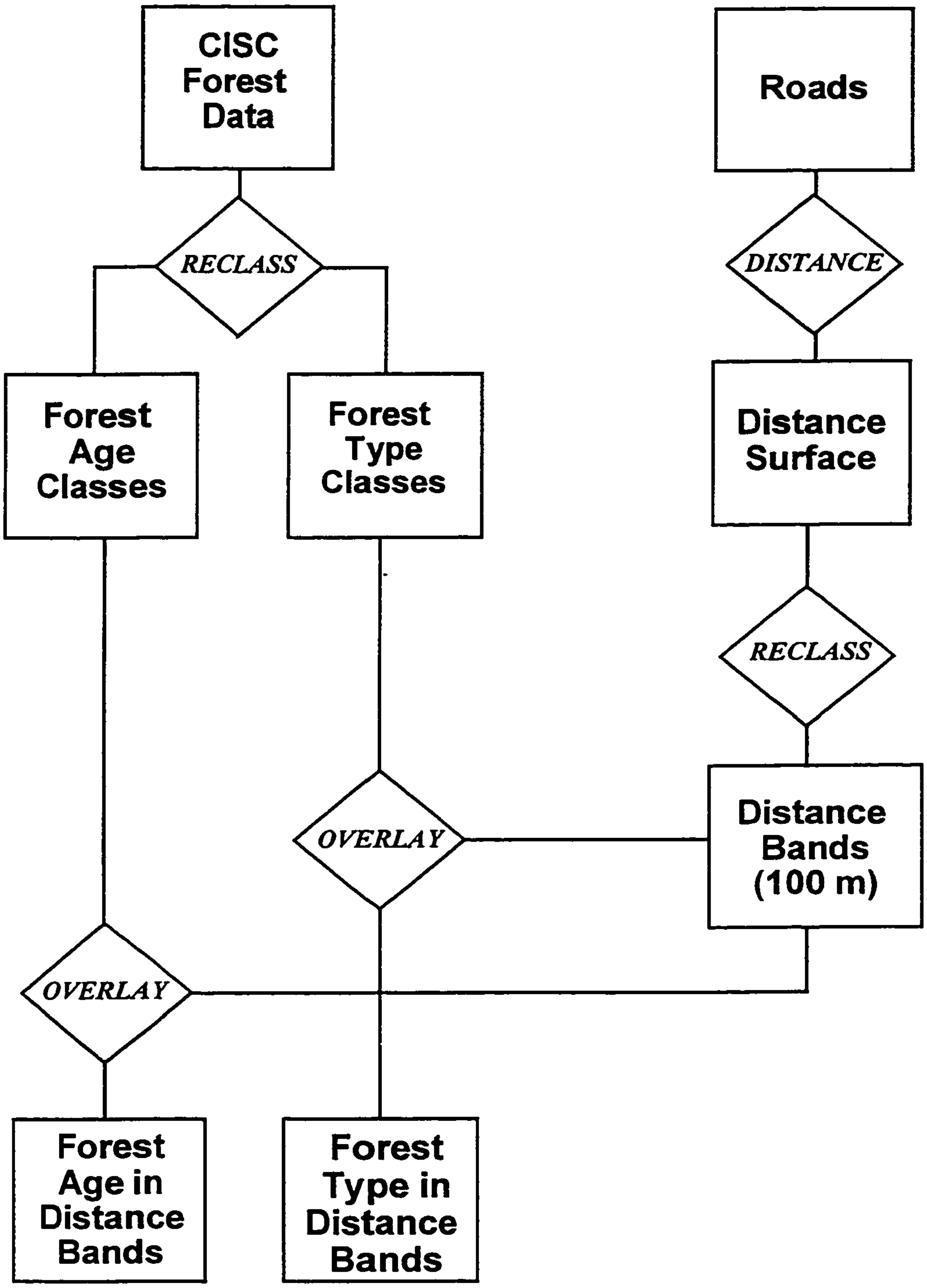


Fig. 2


CISC Forest Data
RECLASS
Roads
DISTANCE
Forest Age Classes
Forest Type Classes
Distance Surface
RECLASS
OVERLAY
Distance Bands (100 m)
OVERLAY
Forest Age in Distance Bands
Forest Type in Distance Bands

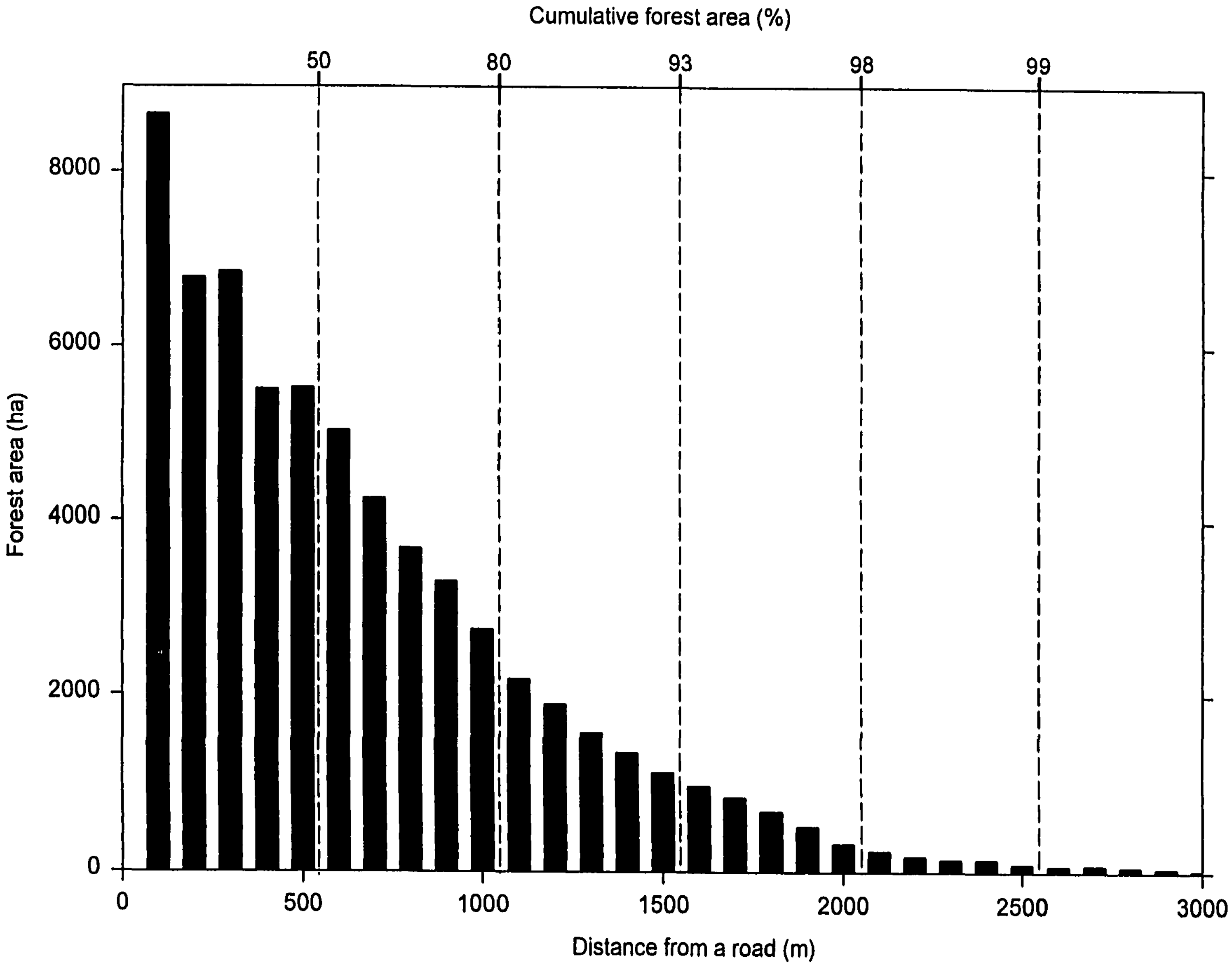

Cumulative forest area (%)
50
80
93
98
99
8000
6000
4000
2000
0
Forest area (ha)
0
500
1000
1500
2000
2500
3000
Distance from a road (m)

Fig. 3

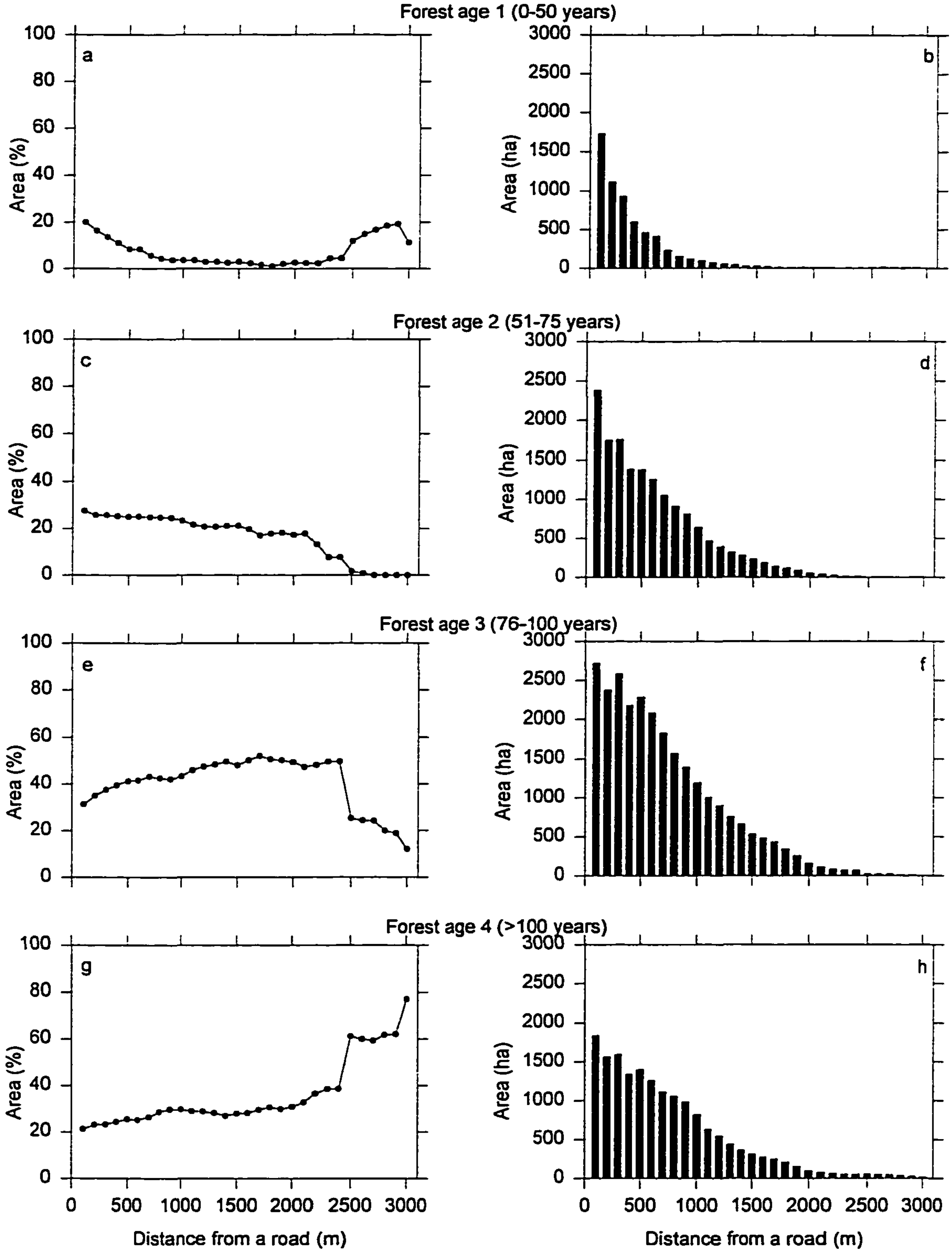

Forest age 1 (0-50 years)
Forest age 2 (51-75 years)
Forest age 3 (76-100 years)
Forest age 4 (>100 years)
a
b
c
d
e
f
g
h
Area (%)
Area (ha)
100
80
60
40
20
0
3000
2500
2000
1500
1000
500
0
0
500
1000
1500
2000
2500
3000
Distance from a road (m)
Distance from a road (m)

Fig. 5

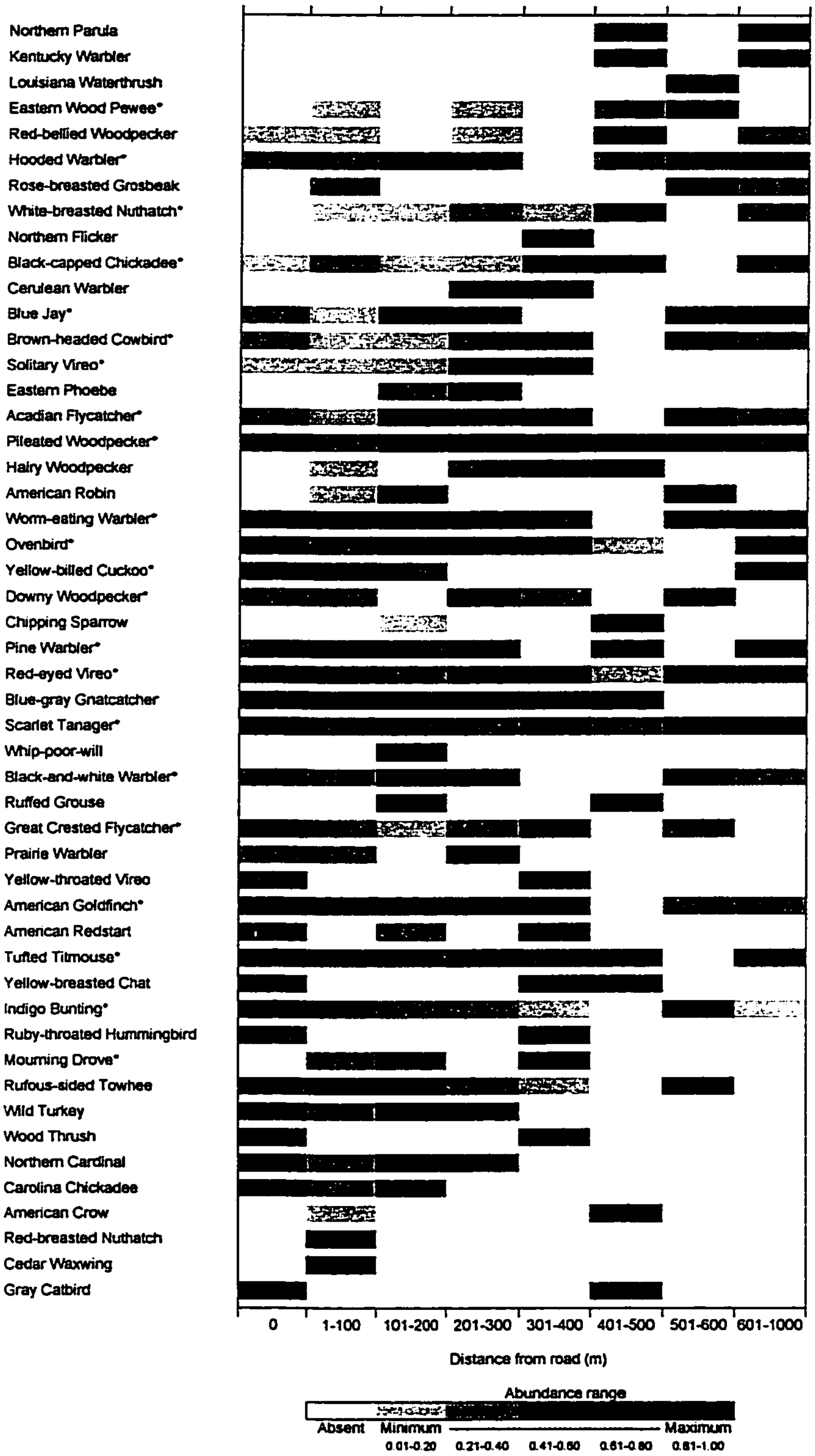
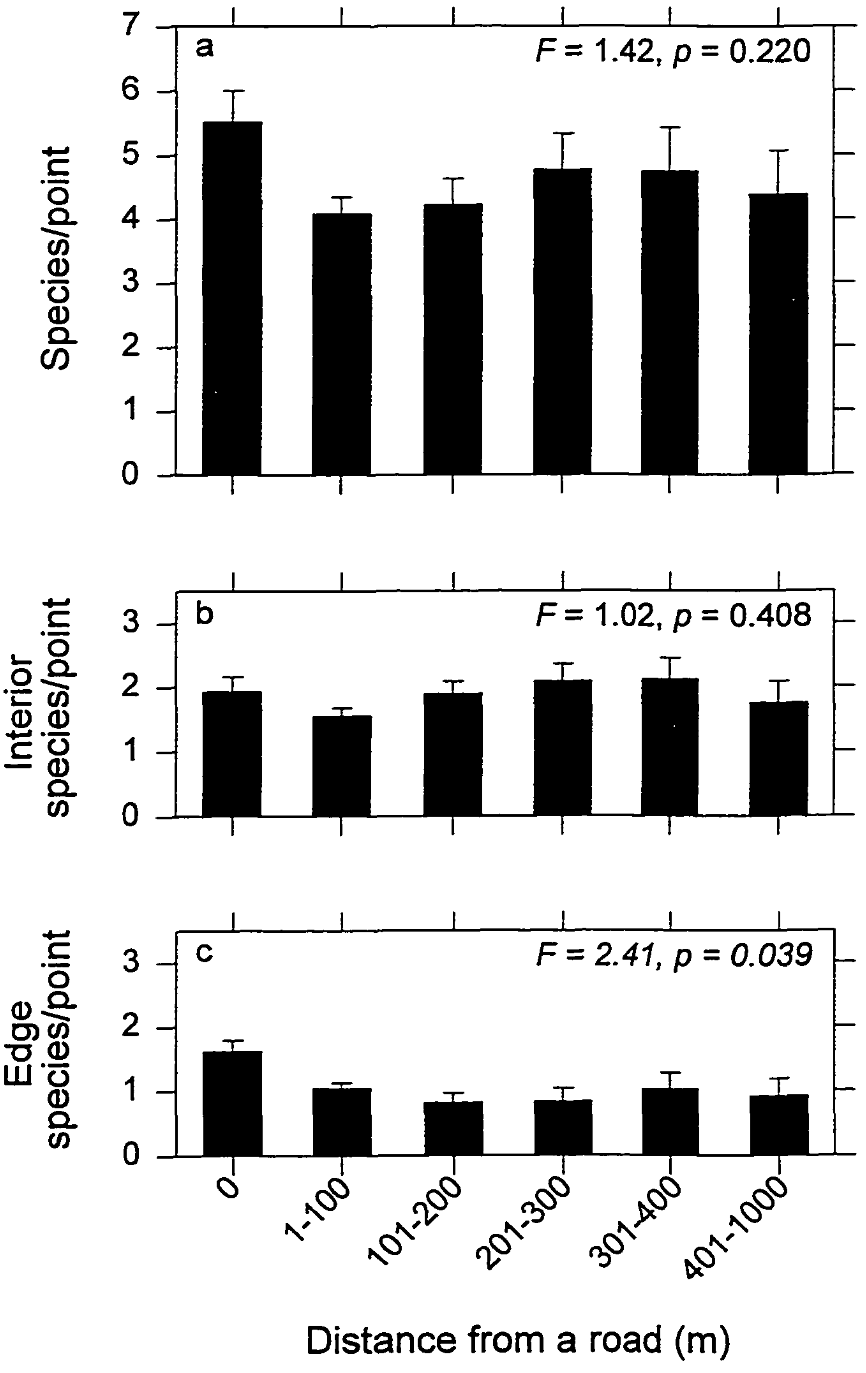

Northern Parula
Kentucky Warbler
Louisiana Waterthrush
Eastern Wood Pewee*
Red-bellied Woodpecker
Hooded Warbler*
Rose-breasted Grosbeak
White-breasted Nuthatch*
Northern Flicker
Black-capped Chickadee*
Cerulean Warbler
Blue Jay*
Brown-headed Cowbird*
Solitary Vireo*
Eastern Phoebe
Acadian Flycatcher*
Pileated Woodpecker*
Hairy Woodpecker
American Robin
Worm-eating Warbler*
Ovenbird*
Yellow-billed Cuckoo*
Downy Woodpecker*
Chipping Sparrow
Pine Warbler*
Red-eyed Vireo*
Blue-gray Gnatcatcher
Scarlet Tanager*
Whip-poor-will
Black-and-white Warbler*
Ruffed Grouse
Great Crested Flycatcher*
Prairie Warbler
Yellow-throated Vireo
American Goldfinch*
American Redstart
Tufted Titmouse*
Yellow-breasted Chat
Indigo Bunting*
Ruby-throated Hummingbird
Mourning Drove*
Rufous-sided Towhee
Wild Turkey
Wood Thrush
Northern Cardinal
Carolina Chickadee
American Crow
Red-breasted Nuthatch
Cedar Waxwing
Gray Catbird
0
1-100
101-200
201-300
301-400
401-500
501-600
601-1000
Distance from road (m)
Abundance range
Absent
Minimum
Maximum
0.01-0.20
0.21-0.40
0.41-0.60
0.61-0.80
0.81-1.00

Fig. 6


Species/point
7
6
5
4
3
2
1
0
a
F = 1.42, p = 0.220
Interior species/point
3
2
1
0
b
F = 1.02, p = 0.408
Edge species/point
3
2
1
0
c
F = 2.41, p = 0.039
0
1-100
101-200
201-300
301-400
401-1000
Distance from a road (m)

Chapter 2

Running head: Spatial extent, accuracy, and landscape pattern

Comparison of spatial extent, accuracy, and landscape pattern in current forest resource maps of the Appalachians

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Abstract Forest-managing agencies in the Appalachian Mountains of the eastern United States have extensive spatial databases that are frequently used for landscape studies and management, but there is little information on the accuracy and usefulness of this data. Additionally, these spatial data have been acquired over areas much larger than the usual forest management units in National Forests of the Appalachian Mountains, and mapping at such large geographic areas may not afford the detail necessary to include resources that are rare and dispersed. We produced a landcover map of a forest management unit on Little Mountain in the George Washington National Forest (GWNF) and compared its accuracy and landscape pattern to the accuracy of two other maps produced from currently available forest resource databases: the Southern Appalachian Assessment (SAA); and Continuous Inventory of Stand Condition (CISC). The maps are different in spatial extent, data sources and purpose of mapping. The differences in accuracy between the maps are mostly a function of map extent. Overall accuracy is highest for the Little Mountain map (map extent: 21,882 ha), followed by the CISC map (439,705 ha) and the SAA map (15.15 million ha). Spatial extent of mapping also affects landscape patterns. The Little Mountain map has a more heterogeneous landscape with more patches and a higher diversity in patch types than either SAA or CISC. The SAA and CISC maps underestimated landcover types that occur in small patches, are rare, or are dispersed. Because management practices in the GWNF occur at scales ranging from 10-40 ha, the usefulness of CISC and SAA for studies on the landscape effects of this management may be limited. Our results demonstrate the need to evaluate the accuracy of spatial databases prior to their use in landscape studies or forest management.

Keywords: spatial extent, scale, landscape structure, GIS, remote sensing, forest management, ecosystem management, accuracy.

Managing and studying forests at the ecosystem level requires the creation and maintenance of a database that can be used to quantify and monitor landscape structure and its effects on the ecosystem (e.g. Franklin and Forman 1987, Turner 1990, Mladenoff et al. 1993, Spies et al. 1994). Forest-managing agencies in the United States have extensive spatial databases, such as the Southern Appalachian Assessment (SAA) and the Continuous Inventory of Stand Condition (CISC), that are frequently used for landscape studies and ecosystem management, but information on the accuracy and usefulness of the data is not available. A major limitation of data sets such as CISC and SAA may be that they were produced by mapping forest resources over large geographic areas: the Southern Region of the U.S. Forest Service and a multistate region in the southern Appalachian Mountains, respectively (Hermann 1996, SAMAB 1996). However, most management decision in the National Forests of the eastern United States are made for much smaller geographic areas, such as a ranger district (60,000-76,000 ha in GWNF) or a timber management unit (10-40 ha in GWNF; George Washington National Forest 1993). Resource data that was collected over geographic areas larger than a ranger district or timber management unit may not be suitable for effective management, because the spatial extent of map data influences the amount of detail as well as the landscape pattern that can be described (Meentemeyer and Box 1987, Turner et al. 1989).

We assessed the accuracy and usefulness of two geographic data sets (SAA and CISC) that are currently used for ecological studies and forest management in the Southern Region of the U.S. Forest Service, by comparing them to a landcover map produced for landscape ecological studies on Little Mountain, a timber management unit extending across the Warm Springs Ranger District and James River Ranger District of the George Washington National Forest, Virginia, USA. We used extensive ground-surveys to assess the thematic accuracy of all three maps and determined differences in landscape patterns using a Geographic Information System and FRAGSTATS (McGarigal and Marks 1995), a landscape analysis program.

Study area

Our study area is on Little Mountain in the Warm Springs and James River Ranger Districts of George Washington National Forest (GWNF), Virginia (Fig. 1). The GWNF manages a total forest area of 429,705 ha, with a portion (36,855 ha) designated as timber management areas (George Washington National Forest 1993).

Little Mountain is located in a timber management area. Federal forests on Little Mountain stretch over an area that is 8 km by 4 km, comprising the west-facing slopes of the mountain with a range of elevation from 600 to 850 m (Fig. 2). According to the CISC data, the U.S. Forest Service manages 148 distinct forest stands on Little Mountain that vary in age and vegetation characteristics. Ages of forest stands range from 1 to 180 years depending on the date of the last timber harvest.

Methods

Digital data

We used three different geographic data sets to produce and compare maps. Because the data sets came from different sources they differ in several characteristics (Table 1), such as data type (raster vs. vector data), geographic projection, spatial extent of the area mapped, and thematic classes used in the classification.

The Southern Appalachian Assessment (SAA) was coordinated by the Southern Appalachian Man and Biosphere Project (SAMAB) and had the support of government agencies and private organizations (SAMAB 1996). The assessment was designed to compile and create data on the environment of the southern Appalachian Mountains and to provide land managers with comprehensive data based on boundaries of ecosystems rather than on administrative boundaries (Hermann 1996, SAMAB 1996; Table 1). While the SAA recognized the need to facilitate management at the landscape scale, the database concentrated on a regional assessment of the entire southern Appalachian Mountains, a spatial extent much larger than a ranger district. The SAA covers an area of approximately 15.15 million ha, in a five-state region. A combination of 14 multispectral and multitemporal Landsat TM images was entered in remote-sensing analyses to classify ecosystems into 16 broad landcover classes (Hermann 1996). Image classification was performed on a multitemporal and multispectral image that was produced by combining spectral bands 3, 4, 7, and a ratio of band 3 and 4 from a summer and a fall image. In order to separate developed and agricultural areas from other landcover categories, image stratification was used. The remaining areas were entered into an unsupervised classification using the ISODATA clustering algorithm (ERDAS 1997) to form 25 spectral clusters. Clusters were assigned to landcover classes using aerial photography and ground-truthing. For our study, the SAA data was projected to a UTM grid using NAD27.

In the Southeastern Region of the U.S. Forest Service, the Continued Inventory of Stand Condition (CISC) is used as geographic database for management decisions concerning timber harvest and natural-resource management. CISC was designed to provide information for silvicultural prescriptions (Table 1). The database was created by delineating and digitizing forest stands on aerial photos at the 1:24,000 scale. The digitized data were registered to ownerships, streams, roads, and other coincident coverages. The classification of forest types in CISC was based on one or more species of trees dominating the canopy and followed the forest definitions by the Society of American Foresters (Eyre 1980). A major drawback to using CISC data for ecosystem management is the restriction of the data to federal lands, which results in administrative boundaries that may not be biologically meaningful. For use in our study, the polygon data from CISC were converted to raster format with a 30-m cell size and projected to a UTM grid with NAD27.

To study the effects of landscape patterns on the ecology of small mammals and songbirds, we produced a landcover map of Little Mountain (LM) in our study region by classifying a Landsat TM image in remote sensing analyses (Table 1; Fig. 2). Because habitat selection in small mammals and songbirds often is strongly influenced by structure and successional stage of forest vegetation (MacArthur and MacArthur 1961, Mills et al. 1991), the classification system for our landcover map focused on forest structure and succession rather than on plant species composition (Table 2). The GWNF provided a Landsat TM (bands 1, 2, 3, 4, 5, 7) scene that was taken on 14 September 1991 and included the study area. The same image was previously used in the SAA for the classification of forest types. We reduced the size of the image to an area of 21,882 ha, including Little Mountain and the adjacent valleys (Fig. 2). To summarize the information of the spectral bands of the Landsat imagery, we applied principal components analysis to the data (ERDAS 1997). Prior to the principal components analysis we standardized the spectral data to a mean of zero and a standard deviation of one. For unsupervised classification of the data into 50 clusters, we used ISODATA clustering on the values derived from the first three principal components (ERDAS 1997). Each cluster was assigned to one of the landcover classes in our classification system (Table 2). Assignment was accomplished by using aerial photographs and habitat information collected at 85 reference points. Forest types were identified at higher levels of classification to distinguish between successional stages. Successional stages were estimated for selected areas during site visits based on observer experience and information on forest ages provided by the U.S. Forest Service. This information was used to guide the classification of the satellite image into a landcover map.

Comparison of thematic accuracy

The quality of the landcover classifications can be estimated with ground-truthing and accuracy assessments (Congalton 1991, Lillesand and Kiefer 1994). In an accuracy assessment, landcover types at known locations in the field are compared to landcover types displayed at the same location on the map (Lillesand and Kiefer 1994, ERDAS 1997). We estimated a relative accuracy by comparing our landcover map with previously produced maps for forest vegetation in the CISC and SAA (Fig. 3).

Classification systems in remote sensing are generally organized in a hierarchical manner so that categories can be aggregated (Lillesand and Kiefer 1994). Because the data-acquisition techniques and data sources differed for SAA, CISC, and LM, we aggregated classes to the lowest common category and restricted comparisons of accuracies to areas that were shared in the data sources. We made no attempt to contrast the accuracies between CISC and SAA because our main interest was in determining how accurate our landcover map is relative to the other data sets.

Comparisons between LM and SAA were restricted to common landcover categories, including deciduous forest, mixed coniferous-deciduous forest, coniferous forest, water, barren, pasture, field, and developed (Table 2 and 3). We omitted SAA landcover types that were not present in the study region, such as northern hardwood forest or montane spruce-fir forest.

CISC is restricted to forested land within the boundaries of National Forests, and comparisons between CISC and LM were confined to areas common in both data sets (Fig. 3). We aggregated the CISC data into categories that divided the forests by major forest type (deciduous, mixed deciduous-coniferous, and coniferous), and successional stage or age (early successional, 0-75 years; mid-successional, 76-120 years; and mature, >120 years; Table 4).

For the accuracy assessment of SAA, CISC, and LM, we used a stratified-random sampling procedures based on the relative area covered by landcover types to predetermine the locations of 500 points. Field teams visited 334 of the selected points using a GPS and assigned the point to a habitat category according to our classification scheme.

We calculated an error matrix to determine the accuracy of the LM map. User's accuracies, the percentage of picture elements (pixels) in a landcover category that belonged to that category during ground-truthing, were used to contrast accuracies between LM, SAA and CISC maps. Overall accuracy, the percentage of reference points in all landcover categories that were classified correctly, also was determined. To test for significance in the difference in overall accuracy between the data sets, we employed a chi-square test with the null hypothesis that percent error is not significantly different between the maps.

Landscape analyses

When comparing landscape patterns for the three maps, we used FRAGSTATS–a landscape-analysis program available through the Internet (McGarigal and Marks 1995). Landscape indices calculated with FRAGSTATS included: number of patches, mean patch size, mean nearest neighbor, Shannon diversity, richness, and contagion (Table 5). For the FRAGSTATS analyses, we used the original classification system for LM (Table 2), and the classification systems for SAA and CISC as described in Table 3 and 4, respectively. The analyses were also restricted to the area common in all data sets, which corresponds to the area of the CISC data on Little Mountain (Fig. 3).

Results

Comparison of accuracy among LM, SAA, and CISC

Deciduous 2 is the most common landcover category in the LM map, followed by deciduous 1, and pasture (Table 6). Together these categories cover over 54% of the study region. Overall accuracy for the LM map is 76% (Table 7). Of the landcover types that have more than 20 reference points from ground-truthing (column totals; Table 7), pasture has the highest user's accuracy, followed by mixed 1, mixed 2, deciduous 1, coniferous 1, and deciduous 2. No category has a user's accuracy below 70%.

When landcover categories are aggregated to assure similarity in the land features depicted on the maps, overall accuracies are significantly higher for the LM map than for either the SAA map ($\underline{X}^2=95.62$, $\underline{df}=1$, $\underline{N}=670$, $\underline{P}<0.001$) or the CISC map ($\underline{X}^2=40.98$, $\underline{df}=1$, $\underline{N}=434$, $\underline{P}<0.001$). User's accuracies for different landcover categories in the LM map generally are higher than user's accuracies for the same landcover categories of SAA or CISC maps (Table 8). Except for deciduous forest types, the LM map has higher user's accuracies for all landcover categories when it is compared to the SAA map (Table 8). The CISC map has slightly higher user's accuracies for mixed 1 forests, but user's accuracies for all other landcover categories are considerably lower for the CISC map than for the LM map (Table 8).

The differences in accuracy between the maps are a function of map extent. Accuracy in depicting deciduous, mixed deciduous-coniferous, and coniferous forests on

Little Mountain generally decreases with increases in spatial extent of the original mapping (Fig. 4). LM maps that were produced for Little Mountain and cover an area of 21,882 ha are most accurate, followed by CISC and SAA that extend over areas of 439,705 and 15,154,857 ha, respectively.

Visual comparisons of the maps emphasize these findings (Fig. 3). SAA was created for regional assessments and planning, but is coarse at the spatial extent of a management unit such as Little Mountain. Landcover types that are typically found only in small patches, such as mixed and coniferous forests, have the lowest user's accuracies in SAA maps (Table 8). Visual comparison shows that these land types cover much less area in the SAA map than in the LM or CISC maps and are probably underestimated in the SAA map. CISC is intended for management at the scale of Little Mountain, but treats forests as discrete polygons representing forest stands. This results in low user's accuracies for many forest types (Table 8). Visual comparison of the CISC with the more accurate LM map shows that CISC overestimates some landcover types, such as mature deciduous forest (deciduous 3), and underestimates common forest types, such as deciduous 1 and 2 (Fig. 3).

Landscape structure comparison of LM, SAA, and CISC

The higher accuracy and detail in the LM map is also reflected in the analyses of landscape patterns for the three geographic data sets (Table 9). Landscapes mapped over smaller areas can include more detail and provide higher thematic accuracy. This results in an increased complexity in the landscape structure represented in the map. The LM map shows a more heterogeneous landscape with more patches and a higher diversity in patch types than CISC or SAA. The increased patchiness also is reflected in smaller mean patch sizes and shorter mean nearest neighbor distances. Fractal dimension is a shape measure that describes the complexity of the perimeters of patches. While the LM is much more heterogeneous, there are only small differences in fractal dimension between the maps.

Discussion

Research in geography and remote sensing stresses the importance of assessing the accuracy of landcover classification (Congalton 1991). Wildlife and land managers often use landcover maps without knowledge of their accuracy because assessing the accuracy of thematic maps can be complex and restricted by methods of ground-data collection, classification schemes, spatial autocorrelation, sample size, and sampling scheme (Congalton 1991). Our study demonstrates the importance of assessing the thematic accuracy of landcover maps prior to their use in landscape ecological studies. The results from our analyses show that the two main data sets available for landscape management of U.S. Forest Service land in Virginia, SAA and CISC, are limited in their thematic accuracy. If thematic accuracy in a map is low for the focal-patch types, the results from landscape analyses will have little value.

We aggregated landcover types into very broad classes for the comparison of accuracies for the different maps. Generally, coarse landcover classifications should yield better accuracies in classification than fine divisions because it is easier to divide forests into main categories of deciduous, mixed deciduous-coniferous and coniferous forest, than to divide them into subtypes, such as mixed mesophytic hardwood forest and oak forest. Despite the broad categories used in the comparison, the LM landcover classification was consistently more accurate than either SAA or CISC.

The biggest differences among the three landcover maps involve the extent of mapping. The most obvious effect of differences in the extent is a loss or gain of detail (Meentemeyer and Box 1987). Maps that are produced over large areas often have to reduce detail and increase the size of the smallest area that can be displayed. This is due to the amount of reduction necessary to still display and store the information of the entire map. Additionally, variation in atmospheric conditions and spectral responses of similar vegetation communities over large spatial areas, make it difficult to use remote sensing for a detailed community mapping of large areas. As a consequence, increasing the spatial extent of the mapping results in a decline of the number of forest types that can be differentiated at the stand level. Also, there will be a reduction in thematic accuracy, a loss of detail in spatial pattern, and a simplification of landscape structure.

The degree of thematic accuracy may not always be the best measure for the usefulness of a geographic data set in landscape analyses. Much of the thematic error associated with an image may occur along boundaries between habitat types. Many of these errors may balance out without actually altering the landscape pattern as expressed in mean patch size, mean nearest neighbor, etc. However, even small errors in delineating habitat types may have a dramatic effect on landscape structure, if these errors make small patches of dispersed and rare habitat types disappear. For these reasons, we demonstrated the importance of comparing landscape structure between maps of the same study area that were derived from geographic data sets that covered areas of different spatial extents.

Spatial scale, defined as spatial extent (Turner et al. 1989), and resolution, defined as grain size, affect the values of landscape indices derived from maps. Turner et al. (1989) examined the effects of changing spatial extent and grain size in maps that were used to analyze landscape patterns. At larger extents and smaller grain sizes, rare landcover types are generally lost. Rare landcover types that are spatially dispersed are most dramatically underestimated. The results from our study support these observations and demonstrate that landscape patterns are qualitatively and quantitatively different between the three maps. Most importantly, information on rare and dispersed landcover types are lost in the SAA and CISC maps. Rare and dispersed landcover types also have the lowest thematic accuracies in the CISC and SAA maps. For example, the SAA and CISC maps severely underestimate the amount of coniferous forest. Also, the CISC map delineates large tracts of mature deciduous forests that in reality are large tracts of midsuccessional deciduous forests with small pockets of mature forest.

Landscape patterns also are affected by the extent of mapping in our study. Because of the loss of detail, average patch size is increased and diversity is reduced for SAA and CISC maps. Average patch sizes calculated from CISC and SAA maps are 30 and 82 ha, respectively. Management actions, such as timber harvest or prescribed burning, in the GWNF are restricted to areas between 10-40 ha (George Washington National Forest 1993). Changes in the landscape structure caused by this type of management are small in size compared to the patches mapped in CISC and SAA. This may lead to an underestimation of landcover change over time.

Most ecosystem characteristics and functions are best managed at a landscape level and there is evidence that landscape structure affects populations dynamics of species (Pulliam 1988, Danielson 1991, McGarigal and McComb 1995, Delattre et al. 1996), disturbance regimes (Baker 1992), nutrient cycling (Naiman et al. 1993), and primary production (Turner 1987). The spatial scale for landscape management needs to be large enough to comprise the full spatial heterogeneity of the system and yet small enough to maintain adequate detail for assessments of the effects of current management on the landscape structure. Management practices in the GWNF, such as prescribed burning or timber harvest, occur at scales ranging from 10-40 ha (George Washington National Forest 1993) and result in patch sizes that are rarely exceeded by the frequent natural disturbances (Runkle 1982, Runkle 1985, Phillips and Shure 1990). Thus, landscape structure for the mesic and xeric forests of the Southern Appalachian should probably be quantified for areas that include the 10-40 ha management units, but are not larger than a single ranger district (ca. 65,000-76,000 ha). The usefulness of CISC and SAA for such purposes is limited, and forests need to be mapped at smaller spatial scales to provide the critical information needed for effective ecosystem management in the forests of the Appalachian Mountains.

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Table 1. Characteristics of digital geographic data available for landscape studies on Little Mountain.

	Geographic data set		
Characteristic	**Southern Appalachian Assessment (SAA)**	**Continuous Inventory of Stand Condition (CISC)**	**Little Mountain (LM)**
Purpose	Aggregate and create land information data for ecological management plans in Southern Appalachians	Forest stand management	Research on how forest management changes landscape patterns
Data source	Landsat TM (14 scenes; acquired between 1991 and 1993)	Aerial photography (1:24,000 scale)	Landsat TM (subset from a single scene; acquired in 1993)
Study area	Southern Appalachian Mountains in Virginia, West Virginia, North Carolina, Georgia and Alabama	George Washington National Forest in Virginia	Timber management area on Little Mountain, Lake Moomaw and surrounding areas in Virginia
Extent	15,154,857 ha	429,705 ha	21,882 ha
Data type	Raster	Vector	Raster
Resolution	0.81 ha	Unknown	0.09 ha
Distance resolution	30 m	Unknown	30 m

Table 2. Hierarchical classification system for mapping forest types from Landsat TM imagery for Little Mountain.

Level I	Level II	Level III
Forest		
	Deciduous	
		Deciduous 1 (~ 0-75 years)
		Deciduous 2 (~ 76-120 years)
		Deciduous 3 (> 120 years)
	Mixed	
		Mixed 1 (~ 0-75 years)
		Mixed 2 (~ 76-120 years)
	Coniferous	
		Coniferous 1 (~ 0-75 years)
		Coniferous 2 (~ 76-120 years)
Water		
Barren		
Pasture		
Field		
Developed		

Table 3. Hierarchical classification system used to aggregate land classes from Southern Appalachian Assessment (SAA) maps. Comparisons between SAA and Little Mountain (LM) performed using level II classes for forest categories and level I classes for all other landcover categories.

Level I	**Level II**	**Level III**
Forest		
	Deciduous	
		Mixed mesophytic hardwood forest
		Oak forest
		Bottomland hardwood forest
	Mixed	
		White pine/hemlock/hardwood forest
		Mixed pine/hardwood forest
	Coniferous	
		Southern yellow pine forest
Water		
Barren		
Pasture		
	Herbaceous	
	Agriculture-pasture	
Field		
	Agriculture-cropland	
Developed		

Table 4. Hierarchical classification system used to aggregate land classes from Continuous Inventory of Stand Condition (CISC) maps. Comparisons between CISC and Little Mountain (LM) performed using level III classes for forest categories.

Level I	**Level II**	**Level III**	**Level IV**
Forest			
	Deciduous		
		Deciduous 1 (~0-75 years)	
			Post oak-black oak (~0-75 years)
			Chestnut oak (~0-75 years)
			White oak-northern red oak (~0-75 years)
			Scarlet oak (~0-75 years)
			Chestnut oak-scarlet oak (~0-75 years)
		Deciduous 2 (~76-120 years)	
			Post oak-black oak (~76-120 years)
			Chestnut oak (~76-120 years)
			White oak-northern red oak (~76-120 years)
			Scarlet oak (~76-120 years)
			Chestnut oak-scarlet oak (~76-120 years)
		Deciduous 3 (>120 years)	
			Post oak-black oak (>120 years)
			Chestnut oak (>120 years)
			White oak-northern red oak (>120 years)
			Scarlet oak (>120 years)
			Chestnut oak-scarlet oak (>120 years)

Table 4. (Continued).

Level I	**Level II**	**Level III**	**Level IV**
	Mixed		
		Mixed 1 (~0-75 years)	
			White pine-upland hardwood (~0-75 years)
			Pitch pine-oak (~0-75 years)
			Virginia pine-oak (~0-75 years)
			Table mountain pine-oak (~0-75 years)
			Southern red oak-yellow pine (~0-75 years)
			Chestnut oak-scarlet oak-yellow pine (~0-75 years)
		Mixed 2 (~76-120 years)	
			White pine-upland hardwood (~76-120 years)
			Pitch pine-oak (~76-120 years)
			Virginia pine-oak (~76-120 years)
			Table mountain pine-oak (~76-120 years)
			Southern red oak-yellow pine (~76-120 years)
			Chestnut oak-scarlet oak-yellow pine (~76-120 years)
	Coniferous		
		Coniferous 1 (~0-75 years)	
			White (~0-75 years)
			Virginia pine (~0-75 years)
			Pitch pine (~0-75 years)
			Table mountain pine-oak (~0-75 years)

Table 4. (Continued).

Level I	**Level II**	**Level III**	**Level IV**
	Coniferous		
		Coniferous 2 (~76-120 years)	
			White (~76-120 years)
			Virginia pine (~76-120 years)
			Pitch pine (~76-120 years)
			Table mountain pine-oak (~76-120 years)

Table 5. Landscape indices used for analyses at different spatial scales (adapted from McGarigal and Marks 1995).

Landscape index	**Description**	**Formula**[a]
Mean nearest neighbor distance	Mean of all Euclidean distances between patches. Distance calculated in meters from edge to edge between nearest patches of same type.	
Mean patch size	Mean area of patches in hectares.	
Fractal dimension	Measurement of perimeter complexity of patches (fractal dimension are treated as perimeter-area relationships).	$d = 2s$
Richness	Number of different patch types.	
Shannon diversity	Relative measure of diversity in patch types based on frequency and eveness of cells of each patch type present in sampling area.	$H' = -\sum_{i=1}^{n} p_i \cdot \ln(p_i)$
Dominance	Emphasizes deviation from eveness in distribution of patch types within sampling area.	$D = \ln(n) - H'$
Entropy	Measure of dispersion of patches in sampling area. Entropy reaches its maximum when all pixels of an attribute are as far apart as possible.	$ENT = -\sum_{i=1}^{n} \sum_{j=1}^{n} p_{ij} \cdot \ln(p_{ij})$
Contagion	Quantifies degree of clumping within sampling area.	$C = 2 \cdot \ln(n) - ENT$
Angular second moment	Expresses homogeneity of landscape. Homogeneous landscapes have large values.	$ASM = \sum_{i=1}^{n} \sum_{j=1}^{n} (p_{ij})^2$

Table 5. (Continued)

Landscape index	Description	Formula[a]
Contrast	Measurement of contrast or attribute variation between patches of sampling area.	$CON = \sum_{i=1}^{n} \sum_{j=1}^{n} \left[(i-j)^2 \cdot p_{ij}\right]$

[a] Equation variables: d, fractal dimension; s, regression slope between log of patch perimeter and log of patch area; p_i, fraction of sampling area occupied by landcover type I; n, number of landcover types in sampling area; p_{ij}, number of times that landcover types i and j are adjacent when examined in a moving window of 3 x 3 cells.

Table 6. Area and percent area covered by the different landcover categories in the Little Mountain (LM) map.

	Area	
Landcover category	**Hectares**	**Percent**
Deciduous 1	3,198	14.65
Deciduous 2	5,703	26.13
Deciduous 3	824	3.78
Mixed 1	1,434	6.57
Mixed 2	2,132	9.77
Coniferous 1	2,274	10.42
Coniferous 2	676	3.10
Water	803	3.68
Barren	326	1.49
Pasture	3,065	14.04
Field	652	2.99
Developed	740	3.39

Table 7. Error matrix for ground-truthing of Little Mountain (LM) map. Bold values on diagonal indicate numbers of correctly classified points. Nondiagonal values in rows are numbers of points found to be in different landcover categories during ground-truthing than indicated by map. Nondiagonal values in columns are numbers of points found to be in different landcover categories on map than indicated during ground-truthing.

	Ground-truth data													**User's**
Map data	**D1**	**D2**	**D3**	**M1**	**M2**	**C1**	**C2**	**W**	**B**	**P**	**F**	**D**	**Row total**	**accuracy^a (%)**
Deciduous 1(D1)	**35**	9	0	2	2	0	0	0	0	0	0	0	48	73
Deciduous 2 (D2)	7	**73**	3	6	11	1	3	0	0	0	1	0	105	70
Deciduous 3 (D3)	0	3	**12**	0	0	2	0	0	0	0	0	0	17	71
Mixed 1 (M1)	0	0	0	**17**	1	0	0	0	0	0	0	0	18	94
Mixed 2 (M2)	1	5	0	5	**33**	0	1	0	0	0	0	0	45	73
Coniferous 1 (C1)	0	0	0	1	1	**14**	1	0	0	0	0	0	17	82
Coniferous 2 (C2)	0	2	0	0	4	1	**19**	0	0	0	0	0	26	73
Water (W)	0	0	0	0	0	0	0	**3**	0	0	0	0	3	100
Barren (B)	0	0	0	0	0	0	0	0	**4**	0	0	0	4	100
Pasture (P)	0	0	0	1	0	0	0	0	0	**23**	1	0	25	92

Table 7. (Continued).

Map data	Ground-truth data												Row total	User's accuracy[a] (%)
	D1	D2	D3	M1	M2	C1	C2	W	R/G	P	F/B	D		
Field (F)	0	0	0	0	1	0	0	0	0	2	9	0	12	75
Developed (D)	0	0	0	0	0	0	0	0	0	0	2	12	14	86
Column Total	43	92	15	32	53	18	24	3	4	25	13	12	334	-
Producer's accuracy[b] (%)	81	79	80	53	62	78	79	100	100	92	69	100	-	76[c]

[a] User's accuracy. Calculated as sum of row divided by number of correctly classified points in row (cells in diagonal) times 100. Represents percentage of points in same category during ground-truthing as indicated on map.

[b] Producer's accuracy. Calculated as sum of column divided by number of correctly classified points in column (cells in diagonal) times 100. Represents percentage of points classified into same category on map as indicated during ground-truthing.

[c] Overall accuracy. Calculated as sum of diagonal divided by total number of points times 100.

Table 8. Comparison of user's accuracies for maps from Little Mountain (LM) with maps from Southern Appalachian Assessment (SAA) and from Continuous Inventory of Stand Condition (CISC).

	User's accuracy (%)			User's accuracy (%)	
Landcover LM-SAA	**LM**	**SAA**	**Landcover LM-CISC**	**LM**	**CISC**
Deciduous	95	97	Deciduous 1	78	54
Mixed	65	1	Deciduous 2	61	46
Coniferous	83	2	Deciduous 3	82	20
Water	100	67	Mixed 1	94	100
Pasture	92	40	Mixed 2	79	53
Field	69	0	Coniferous 1	70	24
Developed	100	31	Coniferous 2	76	22

Table 9. Landscape patterns for Little Mountain calculated from maps of Little Mountain (LM), Southern Appalachian Assessment (SAA), and Current Inventory of Stands Condition (CISC).

Landscape variable	**SAA**	**CISC**	**LM**
Richness	5	7	10
Shannon diversity	0.10	1.54	1.52
Number of patches	29	78	2249
Mean patch size (ha)	82	30	1
Mean nearest neighbor (m)	573	231	77
Fractal dimension	1.06	1.10	1.07

Fig. 1. Location of study area in the Appalachian Mountains of Virginia, USA.

Fig. 2. Landsat TM false-color composite of study area on Little Mountain.

Fig. 3. Comparisons of landcover maps of Little Mountain produced by Southern Appalachian Assessment (SAA), Continuous Inventory of Stand Condition (CISC), and Little Mountain (LM).

Fig. 4. Plot accuracy for all landcover categories and for forest categories against scale of mapping for Southern Appalachian Assessment (SAA), Continuous Inventory of Stand Condition (CISC), and Little Mountain (LM).

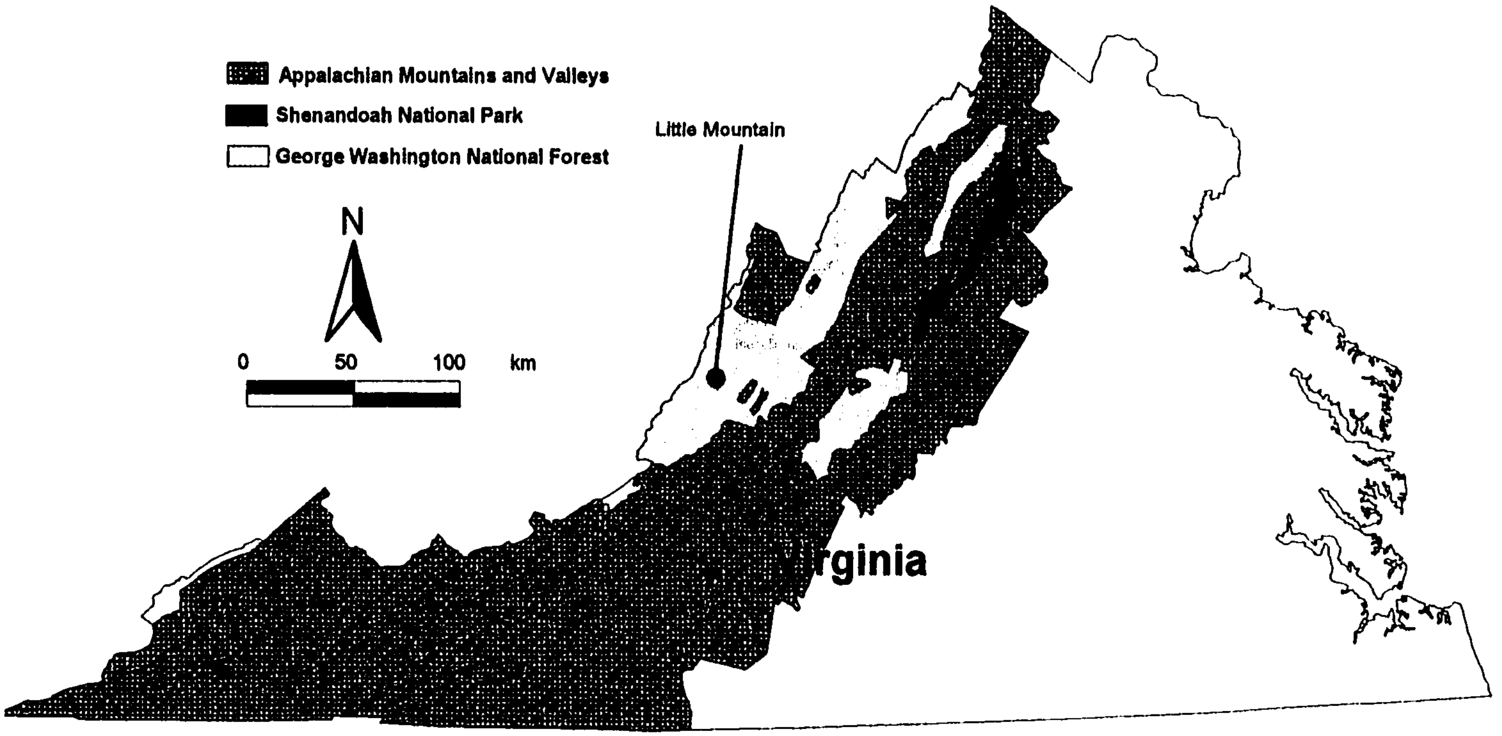

▨ Appalachian Mountains and Valleys
■ Shenandoah National Park
☐ George Washington National Forest
Little Mountain
N
0
50
100
km
Virginia

Fig. 1

Fig. 2

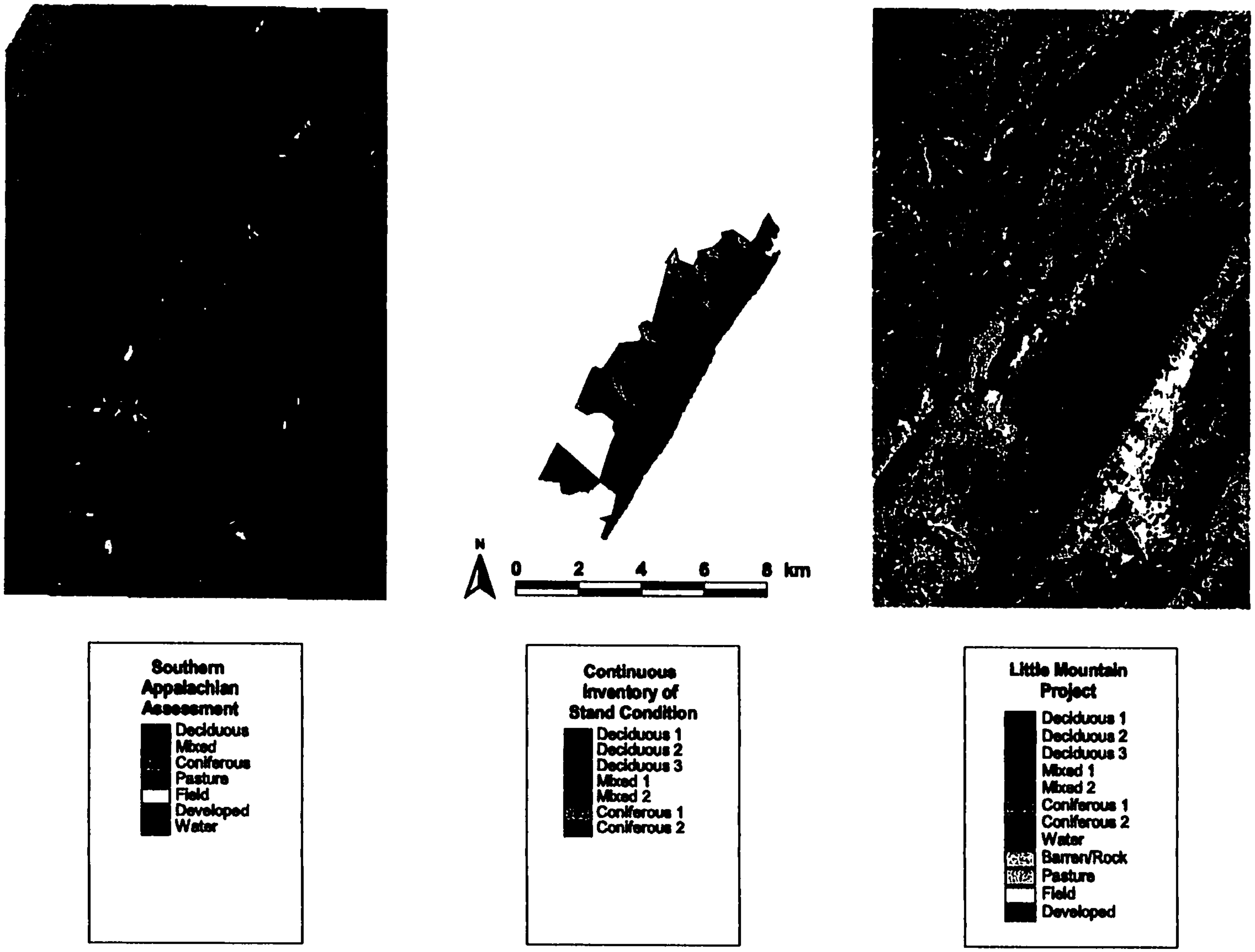
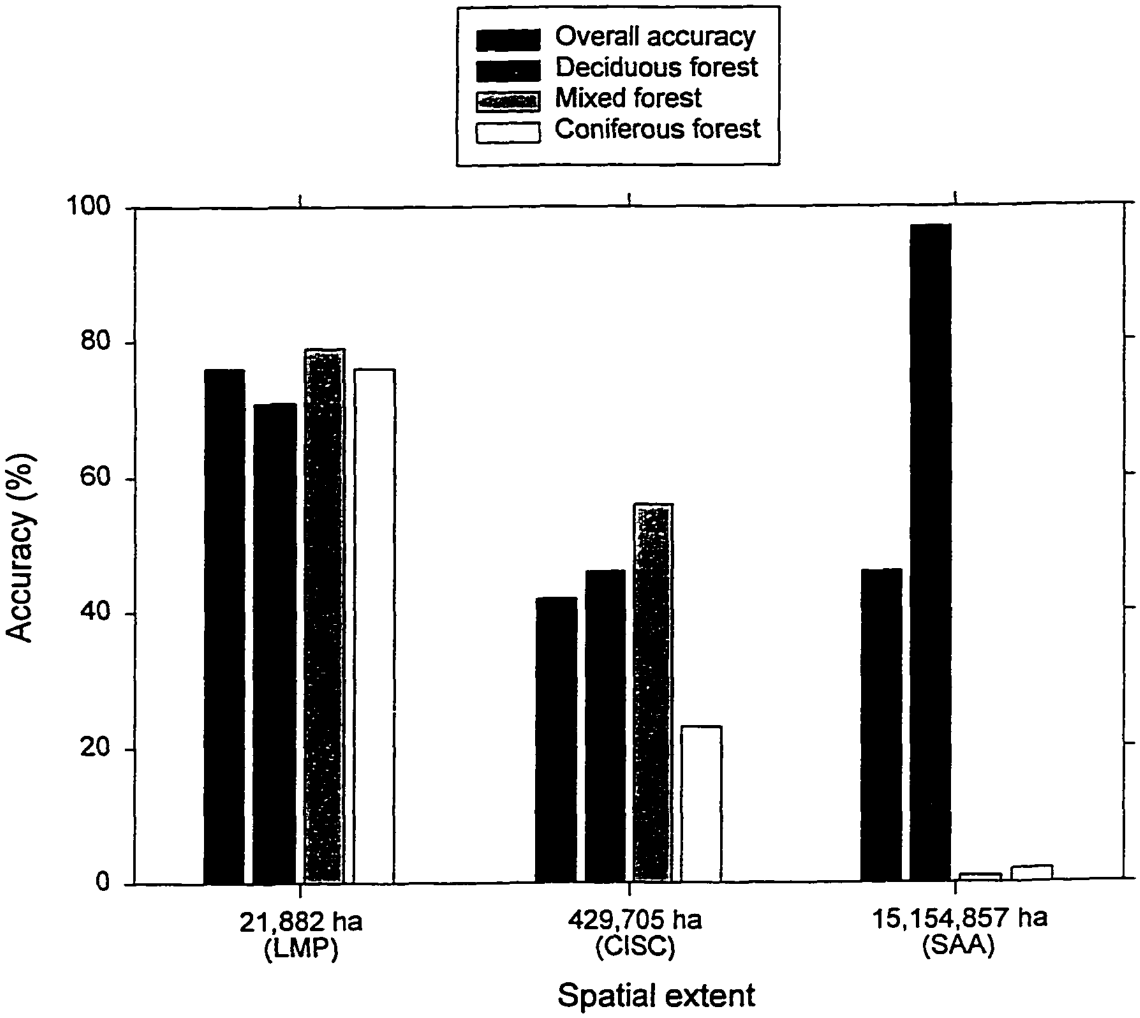

N
0
2
4
6
8 km
Southern Appalachian Assessment
Deciduous
Mixed
Coniferous
Pasture
Field
Developed
Water
Continuous Inventory of Stand Condition
Deciduous 1
Deciduous 2
Deciduous 3
Mixed 1
Mixed 2
Coniferous 1
Coniferous 2
Little Mountain Project
Deciduous 1
Deciduous 2
Deciduous 3
Mixed 1
Mixed 2
Coniferous 1
Coniferous 2
Water
Barren/Rock
Pasture
Field
Developed

Fig. 3

Fig. 4


Overall accuracy
Deciduous forest
Mixed forest
Coniferous forest
100
80
60
40
20
0
Accuracy (%)
21,882 ha
(LMP)
429,705 ha
(CISC)
15,154,857 ha
(SAA)
Spatial extent

Chapter 3

Running head: Spatial scales and logging in a forest mosaic

Effects of scale and logging on landscape structure in a forest mosaic

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Abstract. Landscape structure in a forest mosaic changes with spatial scale (i.e. spatial extent) and thresholds may occur where structure changes markedly. Forest management alters landscape structure and may affect the intensity and location of thresholds. Our purpose was to examine landscape structure at different scales to determine thresholds where landscape structure changes markedly in managed forest mosaics of the Appalachian Mountains in the eastern United States. We also investigated how logging influences landscape structure and whether these management activities change threshold values. Using threshold and autocorrelation analyses, we found that thesholds in landscape indices exist at 400-, 500-, and 800-m intervals from the outer edge of management units in our study region. For landscape indices that consider all landscover categories, such as dominance and contagion, landscape structure and thresholds did not change after logging occurred. Measurements for these overall landscape indices were strongly influenced by midsuccessional deciduous forest, the most common landcover category in the landscape. When restricting analyses for mean patch size and percent cover to individual forest types, thresholds for early-successional forests changed after logging. However, logging changed the landscape structure at small spatial scale, but did not alter the structure of the entire forest mosaic. Previous forest management may already have increased the heterogeneity of the landscape beyond the point where additional small cuts alter the overall structure of the forest. Because measurements for landscape indices yield very different results at different spatial scales, it is important first to identify thresholds in order to determine the appropriate scales for landscape ecological studies. We found that threshold and autocorrelation analyses were simple but powerful tools for the detection of appropriate scales in the managed forest mosaic under study.

Keywords: spatial scale, thresholds, landscape structure, forest mosaic, changing scale, forest logging.

1. Introduction

The structure of the landscape in a ecosystem affects population dynamics of species (Pulliam 1988; Danielson 1991; McGarigal and McComb 1995; Delattre et al. 1996), overall biodiversity (e.g. Holling 1992; Naiman et al. 1993), the spread of disturbance (Franklin and Forman 1987; Turner 1990; Baker 1992a), nutrient cycling (Naiman et al. 1993), and primary production (Turner 1987). However, landscape structure and function are scale dependent (Meentemeyer and Box 1987; Meentemeyer 1989; Turner and Gardner 1990). Landscape indices, such as patch diversity, vary with scale and the importance of an index may change with the size of the area examined (Gardner et al. 1987). Thus, the appropriate scale for landscape ecological studies may depend on the heterogeneity of the landscape, the map source used, and the organisms under study (Wiens 1989; Levin 1992; Turner and Gardner 1990). In this ecological context, scale is absolute and defined by the dimensions (e.g. size, length, shape) of objects or areas (Meentemeyer and Box 1987; Turner et al. 1989). This is not the same as relative cartographic scale that is defined as the ratio of reduction in maps (Meentemeyer and Box 1987).

There are empirical studies that describe how landscape indices change with the spatial scale of geographic data (Turner et al. 1989), and there are several quantitative techniques that can be used to identify spatial scales of landscape patterns (Ver Hoef and Glenn-Lewin 1989; Turner et al. 1990; Pogue 1998). However, these techniques are difficult to apply and understand; they are rarely applied in ecological studies to determine at which spatial scale landscape structure and associated communities should be studied (i.e. Pearson 1993; McGarigal and McComb 1995; Balcom and Yahner 1995; but see Knick and Rotenberry 1994, Pogue 1998).

Meentemeyer and Box (1987) suggested that structural and spatial heterogeneity (e.g. patch size and density) can be used to determine the appropriate scales for landscape studies. However, spatial heterogeneity is unknown before it is measured at a variety of spatial scales. In addition, research by Turner et al. (1989) indicates that indices of landscape structure often do not change linearly, but rather in a stepwise fashion, with stretches of gradual change interspersed by thresholds where marked changes in the indices occur.

We investigated how management changes the landscape structure of a forest mosaic in the Appalachian Mountains of Virginia, U.S.A. This research is important because little is known on how forests in the Appalachian Mountains are affected by past and current management practices at the landscape level. Studies in the coniferous forests of the western United States have demonstrated that changes in landscape structure caused by management are likely to affect ecosystem functions, through increasing fragmentation, patchiness, and complexity of edges (Franklin and Forman 1987; Spies et al. 1994). Because of the scale dependency in landscape structure, we assessed landscape characteristics before and after logging at different spatial scales in a managed forest mosaic of the Appalachian Mountains. We hypothesized: (1) Landscape indices will change gradually with increasing scale until a threshold value is reached after which indices level off (T; Fig. 1A) or change markedly in a different direction (T_1, T_2; Fig. 1B). (2) Differences in landscape structure before and after logging will decrease with increasing scale (Fig. 1A, B). (3) Logging will change threshold values for landscape indices (T', T_1', T_2'; Fig. 1).

2. Methods

2.1. Study area

Our study is part of the Little Mountain Project (LMP) that was designed to investigate how forest management affects small mammals and birds on the landscape scale in forest mosaics of the George Washington National Forest (GWNF) in Virginia. The study area is on Little Mountain in the Warm Springs and James River Ranger Districts of the GWNF (Fig. 2). For the past two centuries the Appalachian forests of the GWNF have been shaped by logging, coal mining, grazing, and human settlement, and the remaining forests comprise a dynamic mosaic of patches varying in forest types and succession. Today, the GWNF manages a total forest area of 429,705 ha, with a portion (36,855 ha) designated for intensive timber harvest (George Washington National Forest 1993).

Little Mountain is located in an area reserved for timber harvest. Federal forests on Little Mountain stretch over an area that is 8 km by 4 km, comprising the west-facing slopes of the mountain with a range of elevation from 600 to 850 m. According to the Continuous Inventory of Stand Condition (CISC), the U.S. federal government manages 148 distinct forest stands on Little Mountain, and these vary in age and vegetation characteristics. Ages of forest stands range from 1 to 180 years based on the date of the last timber harvest.

Between 1994 and 1996, 11 areas (Fig. 3) on Little Mountain, ranging in size from

1.8 to 9.7 ha, were used for shelterwood timber harvest. In shelterwood harvest, the next stand of trees develops under the partial canopy of trees that are left standing after logging (George Washington National Forest 1993). Shelterwoods rely on natural regeneration, stump sprouts, and seeds stored in the forest duff.

2.2. Landcover map

To study the effects of scale and logging on indices of landscape structure, we produced a landcover map of our study region by classifying a Landsat TM image in remote-sensing analyses (Fig. 3). Because our overall study focused on the landscape ecology of small mammals and birds, and because habitat selection by these organisms often is strongly influenced by structure and successional stage of forest vegetation (MacArthur and MacArthur 1961; Mills et al. 1991), the classification system for our landcover map focused on forest structure and succession rather than on plant-species composition (Table 1).

The GWNF provided a Landsat TM scene (bands 1, 2, 3, 4, 5, 7; pixel size, 30 m x 30 m) taken on 14 September 1991. We reduced the size of the image to an area of 21,882 ha, including Little Mountain and the adjacent valleys (Fig. 3). To summarize the spectral information of all spectral bands of the Landsat imagery, we standardized spectral values for each band to a mean of 0 and a standard deviation of 1, and applied principal components analysis. For unsupervised classification with 50 clusters, we used ISODATA clustering on the values derived from the first three principal components (ERDAS 1997). Each cluster was assigned to one of the landcover classes in our classification system (Table 1). Assignment was accomplished by using aerial photos and habitat information collected at 86 reference points. For the determination of successional stages, we used the Continuous Inventory of Stand Condition (CISC) databases of the U.S. Forest Service and site visits. Locations of all ground-control points were determined using differentially corrected data from a Global Positioning System (GPS).

To delineate logging areas, we collected differentially corrected GPS data along the edges. For inclusion into the map, all logged areas were assigned to deciduous 1; all of these timber-harvest areas were categorized as deciduous 2 prior to logging. We did not classify logged areas as bare because vegetation rapidly recolonized the sites. Previous studies have demonstrated that vegetative regeneration in cuts is rapid and reaches 17-58% of the net primary productivity of forest levels within two years after cutting (Phillips and Shure 1990).

Deciduous 2 is the most common landcover category on our map, followed by deciduous 1, and pasture (Table 2). When we determined the overall accuracy of our map using field surveys, we found that our map was accurate at 76% of the control points. Our map was significantly more accurate than two other maps (Leimgruber 1998), one produced from the Continuous Inventory of Stand Condition (a geographic database used by the Southern Region of the U.S. Forest Service) and one produced by the Southern Appalachian Assessment (Hermann 1996, SAMAB 1996).

2.3. Landscape analyses

Landscapes represent mosaics of patches that can be characterized by their structure or pattern. These terms are used interchangeably in landscape ecology to describe the spatial relationships between landscape elements, including size, shape, and arrangement (Turner 1990). In our study, we used the r.le programs of GRASS, the Geographical Resources Analysis Support System (USA-CERL 1991; Baker and Cai 1992; Baker 1994), to quantify patterns in the landscape. A patch was defined as a group of pixels that are connected by at least one interconnecting corner or pixel and that share a common set of attributes (Baker 1994). Patch types were defined by landcover category. Selected landscape indices were computed for all landcover types combined (global indices), or separately for specific landcover types (focal indices).

To determine characteristic spatial scales and thresholds for landscape patterns in the forest mosaic, we measured landscape structure at increasing scales. We increased the size of our sample units by establishing buffers in GRASS (Fig. 4). Landscape indices were first calculated for areas that were within 100 m of logged areas. The spatial extent of these areas was then sequentially increased by adding 100-m-wide buffer strips until the entire area within 1,000 m of logged forest stands was included. We performed additional landscape analyses for areas that included all forest land within 1,500 m and 2,000 m of the logged areas (Fig. 4).

We calculated eight indices for all patch types combined in the landscape (global indices), including (1) richness, (2) Shannon diversity, (3) dominance, (4) mean nearest neighbor, (5) contagion, (6) entropy, (7) contrast, and (8) mean patch size (Table 3).

Because the forest landscape in our study region is dominated by deciduous forest types, we also calculated mean patch size and mean cover for patches of the type deciduous 1, deciduous 2, and deciduous 3 (focal indices).

2.4. Statistical analysis and threshold detection

To compare the response of the landscape indices to changes in the landscape structure at different spatial scales, we used UPGMA (unweighted pair-group method using arithmetic averages; Sneath and Sokal 1973) cluster analysis based on product-moment correlations among indices.

All landscape indices were plotted against spatial scale and we identified thresholds visually from these plots. For the purpose of our study, a threshold was defined as a local minimum or maximum in a landscape index that was proceeded or followed by three data points that did not represent another local minimum or maximum (Fig. 5). A local minimum or maximum is a data point at which the slope of the landscape index against scale changes its direction (Fig. 5). While this definition excludes local minima and maxima that reflected minor variations in the index, it allows us to include threshold points at which landscape indices change markedly (Fig. 5).

We also inspected autocorrelation in the values for landscape indices at different spatial scales to determine whether there were regular patterns in the values that could be used to identify important scales and thresholds (Legendre and Fortin 1989; Turner et al. 1990). For these analyses, we used procedures similar to the computation of a spatial autocorrelation coefficient (Cliff and Ord 1981; Legendre and Fortin 1989). For quantitative variables, autocorrelation can be computed as Moran's _I_ by comparing values of all samples for defined distance classes, also called lags (Turner _et al._ 1990; Legender and Vaudor 1991). We defined six distance classes for spatial scales based on differences in buffers distances. Lag 1 included all samples at 100-m increments of buffers. Buffer increments for lag 2 to 6, were 200, 400, 500, 700, and 1,000 m, respectively. Moran's _I_ varies between -1 and 1, with positive values corresponding to positive autocorrelation between samples. Probability of an autocorrelation coefficient being significantly different from zero also was determined (Legendre and Vaudor 1991)

3. Results

3.1. Thresholds in global landscape indices before logging

We found that global landscape indices can be arranged into five distinct groups based on product-moment correlations and UPGMA cluster analysis (Table 4, Fig. 6). Membership of a landscape index to a particular group was defined by a Pearson correlation-coefficient of 0.89 or higher. This resulted in groupings of indices that increased or decreased with scale in similar ways and had a similar shape in the plots of the landscape indices against scale. The indices in the groups also were similar with regard to the value of thresholds (Fig. 7).

Richness is the only member of group A (Fig. 6) and is characterized by a stepwise increase with thresholds at 400- and 800-m buffer distance (Fig 7A). Richness also shows a strong negative association with mean nearest neighbor, but the only threshold common for these two indices is at 800 m (Table 4, Fig. 7A, H). Group B is constituted by Shannon diversity, entropy and contrast (Fig. 6). All of these indices are highly correlated (Table 4) and show dramatic increases in values after the concordant threshold at 400 m (Fig. 7B, C, D). Contrast has an additional threshold at a buffer distance of 1,500 m after which the values level off. Mean patch size is the sole member of group C (Fig. 6) and is not strongly associated with any of the other indices (Table 4). Mean patch size displays a threshold at the 400-m buffer distance, after which it stays relatively constant with a value of 13 pixels for mean patch size (Fig. 7E). Thus, larger buffers do not include many patches that are larger and a mean patch size of 13 pixels is characteristic for most of the landscape. Group D consists of dominance and contagion (Fig. 6) that have a moderately strong association (Table 4). These indices have common thresholds at 500- and 800-m buffer distances (Fig. 7F, G). After the threshold at 800 m, dominance and contagion decline markedly. The variable mean nearest neighbor constitutes group E (Fig. 6). While it is negatively associated with richness (Table 4), the curve of mean nearest neighbor against scale has a very different shape with a single threshold at 800-m buffer distance. Before the index for mean nearest neighbor reaches the 800-m threshold, it shows a steep decline when plotted against scale.

In summary, seven of the landscape indices reach a threshold at 400- or 500-m buffer size (Fig. 7A, B, C, D, E, F, G) and 4 landscape indices have a threshold at 800-m buffer distance (Fig. 7A, F, G, H). This indicates that the landscape changes most substantially at these buffer distances. The 400- and 500-m thresholds mark the scale at which new landscape elements from the agricultural areas surrounding the forest are included in the landscape indices (Fig 4). At and below these thresholds, the forest areas reach the highest degree of clumping, show the highest homogeneity in forest habitats, and are dominated by few landcover types. Visual inspection of our map shows that these thresholds are influenced largely by the most abundant landcover type–deciduous 2 (Fig. 4).

Final thresholds are reached at a buffer distance of 800 m (or slightly larger as for contrast; Fig. 7D). At these buffer distances a sufficiently large number of patches that dominate in the surrounding landscapes (e.g. pasture, agriculture, and developed) have been included to change the landscape patterns (Fig. 4). Visual inspection of the landcover map shows that beyond these buffer distances the importance of the surrounding matrix habitats increases conspicuously and a large number of pasture and agriculture patches are included in the indices (Fig. 4). Some landscape indices, such as mean patch size, are not affected by these thresholds, suggesting that in areas surrounding the forest, mean patch size is not very different to that in the forested area.

Results from the autocorrelation analyses support these findings. Autocorrelation, calculated as Moran's I, is overall significant for five of the eight landscape indices, including richness, dominance, mean nearest neighbor, contrast and mean patch size (Table 5). Significant autocorrelations were found at 500- and 700-m lags for six of the eight indices. This corresponds to the buffer sizes between 400 and 800 m at which thresholds for landscape indices are found and probably reflects the large scale patterns of forest units that are interspersed by developed and agricultural lands. Significant positive autocorrelations at 100-m increments of buffer distance were found for seven of the eight indices, the exception being dominance (Table 5). Significant autocorrelations for the smallest lag shows that scales that are very similar in size also are similar in landscape characteristics. The results from the threshold and autocorrelation analyses support our hypothesis 1 that landscape indices will change gradually with scale until a threshold value is reached after which the indices change markedly in a different direction or level off.

3.3. Effects of logging on global landscape indices

At small buffer distances, values for most of the landscape indices after logging are changed somewhat, but the overall shape of the curves and the location of the thresholds were affected minimally by logging (Fig. 7A-H). Differences for indices between before and after logging are most pronounced at scales below the 500-m buffer distance (Fig. 7). This finding supports hypothesis 2 that differences in landscape structure before and after logging decreases with increasing scale. However, thresholds at the 400-m buffer distance or greater are not affected by logging and are the same for landscape indices measured before and after logging (Fig. 7). Based on this observation, we reject hypothesis 3: that logging alters the location of thresholds for changes in landscape indices with scale in our study region. This conclusion is also supported by the fact that significant autocorrelation at the 500- and 700-m lags are found for five of the landscape indices after logging (Table 5). Contagion is the sole landscape index that showed significant autocorrelation at these lag distance before logging but not after (Table 5). We conclude that landscape structure changes at small scales after logging, but does not affect the structure of the larger landscape.

3.4. Thresholds in focal landscape indices before logging

Because forests in our study region are predominantly mesic and deciduous, we chose to calculate selected landscape indices for deciduous landcover categories to assess the importance of these landcover types for the global landscape patterns. Mean patch size changes little with increasing scale for deciduous 1 and 3 (Fig. 8A, C). According to our definition, deciduous 1 has thresholds at 300- and 700-m buffer distances, but changes in the slope caused by these thresholds are minor (Fig. 8A). The mean patch size for deciduous 2 is dominant in the landscape and has thresholds at 700- and 900-m buffer distances (Fig. 8B). As pointed out for the global indices, around a buffer distance of 800 m, the patches of the surrounding agricultural land become increasingly more important. The increases for mean patch size of deciduous 2 indicate that there are large patches of deciduous 2 that are only fully included in the landscape indices when the entire forested area is considered. If the sample unit is increased beyond the forest area, mean patch size declines again because additional small patches from the agricultural areas are included.

Percent cover for different forest type shows a similar pattern (Fig. 9). Changes in percent cover of deciduous 1 and 3 with increasing scale are minor, and no distinct thresholds can be detected (Fig. 9A, C). Percent cover for deciduous 2, however, increases until it reaches a threshold at the 500-m buffer distance and then declines (Fig 9B).

As for global indices, these findings are supported by the results from the autocorrelation analyses for focal landscape indices (Table 6). Mean patch size for deciduous 1 shows a significant negative autocorrelation at a lag of 700 m, which corresponds to its threshold at the 700-m buffer distance. Mean patch size for deciduous 2 and percent cover for deciduous 1 are the only focal indices that have overall significant autocorrelation structure (Table 6). All focal indices show positive autocorrelation at the first lag, demonstrating that areas of similar scale will also be similar in landscape structure. The autocorrelation at the first lag also explains the overall significant autocorrelation structure for percent cover of deciduous 1.

We conclude that patches of deciduous 2 have a strong influence on the landscape structure calculated by the global landscape indices. Only the findings for deciduous 2 support our hypothesis 1. Patches of deciduous 1 and 3 comprise a relatively small portion of the landscape and are generally smaller than patches of deciduous 2.

3.5. Effects of logging on focal landscape indices

Mean patch size and percent cover of deciduous 1 and 2 were altered considerably by logging (Figs. 8A, B and 9A, B) . As with other variables, these effects are most pronounced at small scales. For deciduous 2 these changes in mean patch size and percent cover do not affect the location of the thresholds. However, in the case of mean patch size for deciduous 1, new thresholds appear after logging (Figs. 8A and 9A), while thresholds for deciduous 2 remain the same after logging (Figs. 8B and 9B). The mean patch size of deciduous 1 has a new threshold at the 300-m buffer distance, and percent cover for deciduous 1 shows a new threshold at the 800-m buffer distance. These changes in thresholds are easily explained, because logging increases the number of large patches of early successional forest. Deciduous 3 is not affected by the logging (Figs.

8C and 9C). Percent cover and mean patch size for deciduous 1 are the only landscape indices that support hypothesis 3 that logging will alter the location of thresholds. Mean patch size and percent cover for deciduous 1 are also the two focal landscape indices that demonstrate the greatest changes in autocorrelation structure (Table 6).

4. Discussion

4.1. Multiscale landscape structure

The question at which spatial scale to study an ecological system and processes is common in ecology and varies with the characteristics of the system and the questions to be addressed (Wiens 1989; Levin 1992; Pogue 1998). We wanted to evaluate how current shelterwood cutting affects landscape structure and at what spatial scales these changes are most pronounced.

Thresholds are break points at which the values for landscape indices change substantially. Such thresholds exist in our forest mosaics. We showed how thresholds determined from simple plots of landscape indices against spatial scale and autocorrelation analyses can be used to determine appropriate spatial scales for ecological studies. The results from our analyses support hypothesis 1 and 2, that landscape indices have thresholds at increasing scales at which their statistical behavior changes markedly and that after logging landscape structure changes more drastically at smaller spatial scales. Many of the landscape indices used in our study showed similar patterns for thresholds and autocorrelation structure, and are concordant in their way the measurements vary with scale. Thus, important thresholds in the landscape structure can be detected with a variety of landscape indices. As some landscape characteristics (e.g. richness and patchiness) change markedly at the thresholds, other ecological characteristics and processes (e.g. diversity of organisms, flow of nutrients, and energy flow) are likely to exhibit notable changes as well. For ecological studies on the landscape scale, it is important first to identify the threshold scales, since measurements taken at different scales may yield substantially different results. To study the influence of logging on other ecological characteristics, such as species distribution, abundance, and diversity in our study region, we suggest that analyses are conducted at spatial scales below the 400-m buffer distance, as logging in the region under study changes the landscape structure most markedly below these scales (Fig. 10A). To determine the influence of the overall landscape on ecological characteristics, we suggest that the interrelationships are examined across at least three spatial scales: below the 400-m buffer distance, between the 400-m and 800-m buffer distances, and at buffer distances larger than 800 m (Fig. 10B). Because of the differences in landscapes discussed previously, important spatial scales may vary among different landscapes. The techniques we applied, however, will be useful to determine appropriate scales for ecological studies in other landscapes.

There are many quantitative techniques that have been used to determine important spatial patterns and spatial scales in landscapes (for summary, see Turner et al. 1990; Pogue 1998). However, often these techniques are restricted to specific sampling regimes (transects, plots, etc.) and are difficult to interpret and understand. We believe that using thresholds in plots of landscape indices against scale are a useful and parsimonious tool for determining the appropriate spatial scale at which to study landscape ecological questions. Autocorrelation analyses or other quantitative techniques can then be employed to verify the significance of these thresholds. We used Moran's I, an autocorrelation coefficient, as an index that indicates interactions between scales as the sampling units are increased. We showed how thresholds are in concordance with significant autocorrelation between sampling scales and interpret this as indication of important spatial scales in our landscape.

Thresholds and autocorrelation analyses for global landscape indices were not good indicators for the changes that occur in our forest mosaics after logging. After logging, thresholds did not shift and autocorrelation structure did not change substantially for global landcover indices, indicating that the global landscape structure in the forest mosaic of our study region did not change through timber harvest. One explanation for this could be that the landscape structure is already affected by previous, intensive logging and, thus, the heterogeneity changes little after new shelterwood cutting.

An alternative explanation is that changes occurring at the landscape scale were not detected by the global landscape indices we used. A study by Miller et al. (1995) showed that global landscape indices are not always useful in detecting landscape changes. They found that riparian landscapes changed markedly in the amount of area covered by different land types, but that patch size, richness or other global landscape indices did not. When examining focal landscape indices, we found changes in the landscape structure that could be detected with focal indices. The increases in mean patch size and percent cover of deciduous 1 and 2 were the most noticeable changes we detected. Thresholds did shift for mean patch size of and percent cover of deciduous 1. To investigate the influence of management on landscape structure, it may be important to use focal indices on selected landcover types to determine what changes are occurring. For example, while global mean patch size may not change after management, the number of patches for selected landcover types can change substantially as old-growth patches are replaced by clear-cuts.

Generally, common landcover and clumped landcover types will exert the strongest influence on global landscape indices. Conservation goals in the GWNF in Virginia, however, are oriented towards the rare and dispersed natural resources, such as old-growth forest, shale barrens, and table mountain pine communities (George Washington National Forest 1993). Landscape conditions for rare and dispersed types probably are not well reflected by global landscape indices. Also, changes for these communities will most often not be conversions into other types, but alterations in the surrounding forest mosaics that change conditions for flow of matter, microclimate, and dispersal of organisms. For example, in our study mean patch size and percent cover for deciduous 3 did not change because most of the areas that were logged were covered by deciduous 2 forests. However, since the total amount of deciduous 1 forest increased, it is possible that movements of organisms dependent on old forest types become more limited in a landscape that is dominated by early-successional forests.

Landscape structure differs among unmanaged, virgin forests, and managed forests, reflecting differences between natural and human-caused disturbances (Baker 1992; Mladenoff et al. 1993; Turner et al. 1994). Forest management changes landscape patterns and is likely to affect ecosystem functions, through increasing fragmentation, patchiness, and complexity of edges in forests (Franklin and Forman 1987; Spies et al. 1994). Most of the research on landscape structure in forest ecosystems has been conducted in the coniferous ecosystems of the western United States, and relatively little is known about landscape structure in the deciduous forests of the Appalachians. Obtaining similar information for eastern deciduous forest is difficult because little virgin forest is left and the management history is much more complicated due to smaller land parcels and longer periods of settlement and disturbance.

We found a complex landscape structure, with many small patches (the maximum mean patch size was 13 pixels, which equals 1.17 ha), a high diversity in forest types, and few homogenous large stands. There is a greater amount of fine-scale variation in forest types than one would expect based only on the management history of large-scale logging at the beginning of this century. One possible explanation for the relatively high heterogeneity is that, after clear-cutting, the topography, soil quality, and water regime increase divergence of vegetation patches within the clear-cut stands. Over the years of regeneration, relatively frequent small disturbances increase spatial heterogeneity (Runkle 1992). Additionally, forest managers may not always treat forest stands as homogenous units, and parts of previously harvested stands may be managed differently, increasing the overall patchiness of the forest. We have no information on patchiness or structure of virgin mesic deciduous forests of the Southern Appalachian Mountains, and comparisons have not been made between the landscape structure of unmanaged and managed forest. Such studies are urgently needed to determine what forest management techniques produce landscape structures that approximate natural landscapes for forests in the Appalachian Mountains.

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Table 1. Classification system for mapping forest types on Little Mountain from Landsat TM imagery.

Level I	Level II	Level III
Forest		
	Deciduous	
		Deciduous 1 (~ 0-75 years)
		Deciduous 2 (~ 76-120 years)
		Deciduous 3 (> 120 years)
	Mixed	
		Mixed 1 (~ 0-75 years)
		Mixed 2 (~ 76-120 years)
	Coniferous	
		Coniferous 1 (~ 0-75 years)
		Coniferous 2 (~ 76-120 years)
Water		
Barren		
Pasture		
Field		
Developed		

Table 2. Area and percent cover for landcover categories.

	Area	
Landcover category	Hectares	Percent
Deciduous 1	3,198	14.65
Deciduous 2	5,703	26.13
Deciduous 3	824	3.78
Mixed 1	1,434	6.57
Mixed 2	2,132	9.77
Coniferous 1	2,274	10.42
Coniferous 2	676	3.10
Water	803	3.68
Barren	326	1.49
Pasture	3,065	14.04
Field	652	2.99
Developed	740	3.39

Table 3. Landscape indices used for analyses at different spatial scales (adapted from Baker and Cai 1992).

Landscape index	Description	Formula[a]	Reference[b]
1 Richness	Number of different patch types.		1,2
2 Shannon diversity	Relative measure of diversity in patch types based on frequency and eveness of cells of each patch type present in sampling area.	$H' = -\sum_{i=1}^{n} p_i \cdot \ln(p_i)$	1,2,4
3 Dominance	Emphasizes deviation from eveness in distribution of patch types within sampling area.	$D = \ln(n) - H'$	1,2,4
4 Mean nearest neighbor	Mean of all Euclidean distances between patches. Distance calculated in pixels from edge to edge between nearest patches of same type.		1,2
5 Contagion	Quantifies degree of clumping within sampling area.	$C = 2 \cdot \ln(m) - ENT$	1,2,3
6 Entropy	Measure of dispersion of patches in sampling area. Entropy reaches its maximum when all pixels of an attribute are as far apart as possible.	$ENT = -\sum_{i=1}^{n} \sum_{j=1}^{n} p_{ij} \cdot \ln(p_{ij})$	1,2
7 Contrast	Measurement of contrast or attribute variation between patches of sampling area.	$CON = \sum_{i=1}^{n} \sum_{j=1}^{n} \left[(i-j)^2 \cdot P_{ij}\right]$	1,2
8 Mean patch size	Mean area of patches in pixels.		1,2

[a] Equation variables: p_i, fraction of sampling area occupied by landcover type i;; n, number of landcover types in sampling area; p_{ij}, number of times landcover types i and j are adjacent when examined in a moving window of 3 x 3 cells.

[b] Refereces: (1) Baker and Cai 1992; (2) Baker 1994; (3) Krummel et al. 1987; (4) O'Neill et al. 1988.

Table 4. Pearson product-moment coefficients for eight landscape indices based on comparisons across scales.

	Landscape index						
Landscape index	1	2	3	4	5	6	7
1 Richness							
2 Shannon diversity	0.79						
3 Dominance	-0.47	-0.91					
4 Mean nearest neighbor	-0.93	-0.71	0.39				
5 Contagion	-0.06	-0.65	0.89	0.05			
6 Entropy	0.79	0.99	-0.89	-0.73	-0.66		
7 Contrast	0.90	0.92	-0.73	-0.80	-0.38	0.91	
8 Mean patch size	0.60	0.34	-0.08	-0.75	0.05	0.42	0.35

Table 5. Autocorrelation Moran's I in global landscape indices at different spatial scales before and after logging. Overall significance (P) of autocorrelation structure calculated by using most significant P-value in a Bonferoni adjustment. Lags defined as differences in buffer distances (scale) used to measure indices. Numbers of samples given in parenthesis in boxhead. Asterisks indicate local statistical significance of autocorrelation values (*, $P<0.05$; **, $P<0.01$; ***, $P<0.001$).

	Lag (m)						
Landscape index	100 (9)	200 (8)	400 (13)	500 (7)	700 (9)	1000 (7)	Overall P
			Before logging				
1 Richness	0.78**	0.54*	0.04	-0.04	-0.63*	-0.46	0.018*
2 Shannon diversity	0.40*	0.33	0.17	0.69*	-0.11	-0.40	0.078
3 Dominance	0.26	0.23	0.20	0.70**	-0.19	-0.54	0.048*
4 Mean nearest neighbor	0.86***	0.60*	-0.03	-0.33	-0.72*	-0.3	0.005**
5 Contagion	0.54*	0.35	0.03	0.02	-0.76*	-0.77*	0.078
6 Entropy	0.39*	0.32	0.14	0.65*	-0.13	-0.42	0.096
7 Contrast	0.73**	0.44	-0.15	0.03	-0.33	-0.34	0.030*
8 Mean patch size	0.61**	0.17	-0.25	-0.21	-0.44	-0.23	0.012*
No. significant differences	7	2	0	3	3	1	5
			After logging				
1 Richness	0.78**	0.54*	0.04	-0.04	-0.63*	-0.46	0.024*
2 Shannon diversity	0.40*	0.34	0.17	0.67*	-0.11	-0.39	0.084
3 Dominance	0.30	0.22	0.20	0.73**	-0.16	-0.52	0.036*
4 Mean nearest neighbor	0.81**	0.61*	-0.03	-0.34	-0.72*	0.33	0.012*
5 Contagion	0.31	0.16	0.12	0.36	-0.45	-0.55	0.474
6 Entropy	0.36	0.31	0.19	0.70*	-0.07	-0.42	0.072
7 Contrast	0.72**	0.49*	0.00	0.17	-0.35	-0.52	0.030*
8 Mean patch size	0.61**	0.18	-0.24	-0.20	-0.44	-0.24	0.012*
No. significant differences	5	3	0	3	2	0	5

Table 6. Autocorrelation Moran's I in focal landscape indices at different spatial scales before and after logging. Overall significance (P) of autocorrelation structure calculated by using most significant P-value in a Bonferoni adjustment. Lags defined as differences in buffer distances (scale) used to measure indices. Numbers of samples given in parenthesis in boxhead. Asterisks indicate local statistical significance of autocorrelation values (*, P<0.05; **, P<0.01; ***, P<0.001).

	Lag (m)						
Landscape index	100 (9)	200 (8)	400 (13)	500 (7)	700 (9)	1000 (7)	Overall P
Before logging							
Mean patch size							
Deciduous 1	0.39*	-0.50	0.53*	0.29	0.28	-0.08	0.150
Deciduous 2	0.88***	0.51*	-0.12	-0.46	-1.00***	-0.78*	0.001***
Deciduous 3	0.24	0.13	0.10	0.54*	-0.05	-0.09	0.078
Cover							
Deciduous 1	0.91***	0.37	-0.43	-0.61	-0.55	0.03	0.006**
Deciduous 2	0.40*	0.29	0.08	0.55*	-0.18	-0.50	0.192
Deciduous 3	0.55*	-0.26	-0.50*	-0.22	-0.20	0.10	0.090
No. significant differences	5	1	2	2	1	1	2
After logging							
Mean patch size							
Deciduous 1	0.70**	0.57*	-0.03	-0.27	-0.62*	-0.34	0.030*
Deciduous 2	0.93***	0.55*	-0.09	-0.50	-1.00***	-0.77*	0.001***
Deciduous 3	0.27	0.13	0.09	0.52*	0.04	-0.08	0.114
Cover							
Deciduous 1	0.53**	0.24	-0.07	-0.12	-0.41	-0.34	0.012*
Deciduous 2	0.50*	0.25	-0.12	0.01	-0.44	-0.52	0.162
Deciduous 3	0.55*	-0.20	-0.45*	-0.17	-0.22	0.05	0.072
No. significant differences	5	2	1	1	2	1	3

Fig. 1. Hypothetical changes in landscape indices as function of spatial scale and logging. Before logging (solid lines in A and B), landscape indices change gradually at small scales until they reach a threshold (T, T_1) at which they either (A) level off or (B) change drastically in opposite direction. Some landscape indices will change again at one or more additional thresholds (T_2 in panel B) at larger scales. After logging (dashed lines), landscape indices change most drastically at small scales and thresholds are shifted (T', T_1', T_2').

Fig. 2. Location of study region on Little Mountain in the George Washington National Forest of Virginia, USA.

Fig. 3. Landsat TM false-color composite of study area on Little Mountain. White polygons represent management units used for logging.

Fig. 4. Landcover map of Little Mountain produced by classifying Landsat TM imagery. Black and red lines delineate buffer zones used to increase spatial scale. Red lines indicate buffer distances where thresholds in landscape indices detected. White areas represent logged forest areas.

Fig. 5. Hypothetical plot of changes in landscape indices with scale indicating which local minimum/maximum represent a threshold.

Fig. 6. UPGMA cluster analysis based on correlations of landscape indices across spatial scales.

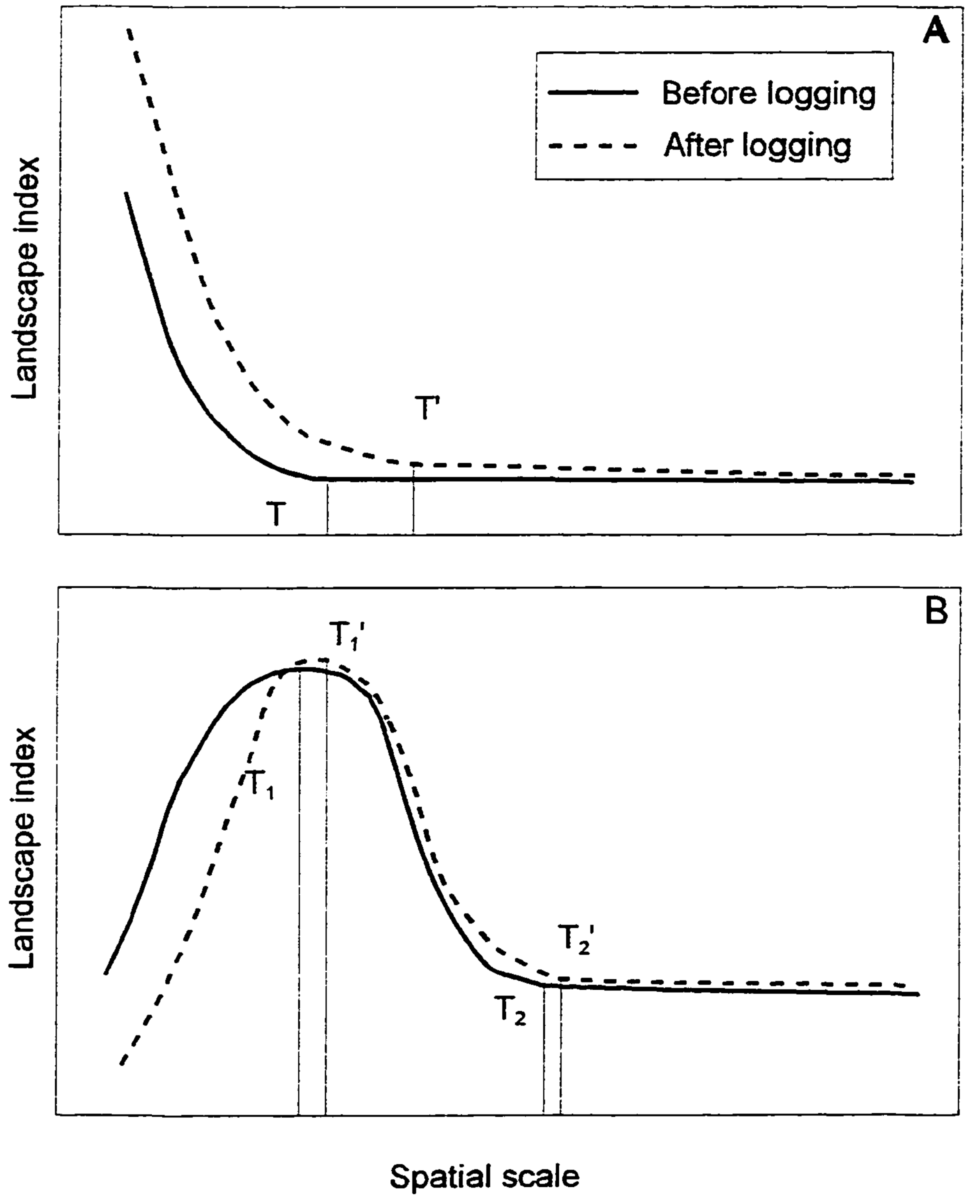
Fig. 7. Global landscape indices plotted against buffer distance for detection of thresholds, where landscape structure changes drastically before and after logging. Droplines indicate buffer distances where thresholds detected.

Fig. 8. Mean patch size for deciduous forests types plotted against buffer distance for detection of thresholds before and after logging. Droplines indicate buffer distances where thresholds detected.

Fig. 9. Percent cover for deciduous forests types plotted against buffer distance for detection of thresholds. Droplines indicate buffer distances where thresholds detected.

Fig. 10. Ranges of spatial scales for landscape ecological studies. Portion A of horizontal axis indicates scales for studies investigating the effects of logging on communities. Portion A and B of horizontal axis indicates scales for studies investigating influence of landscape structure on communities.

Fig. 1


A
Before logging
After logging
Landscape index
T
T'
B
Landscape index
T_1
T_1'
T_2
T_2'
Spatial scale

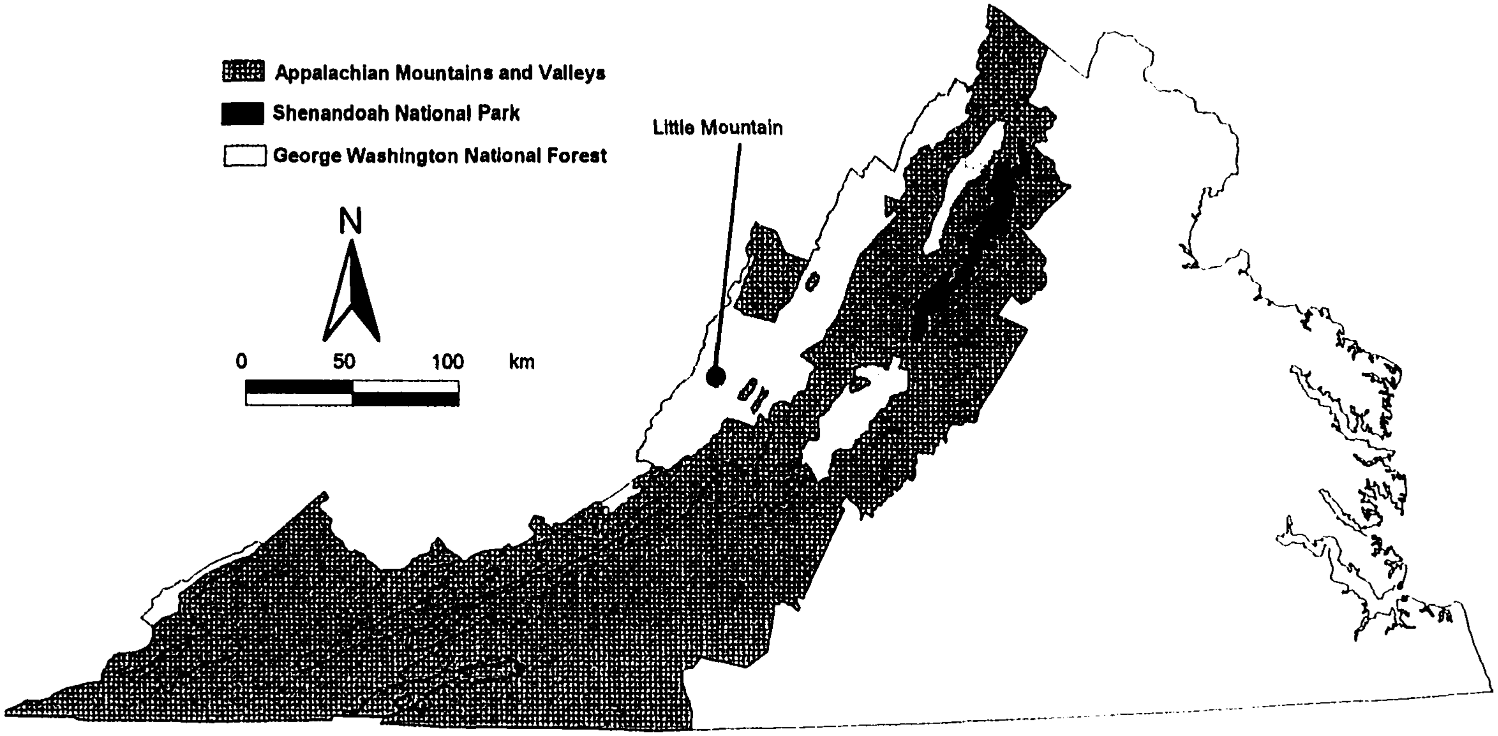
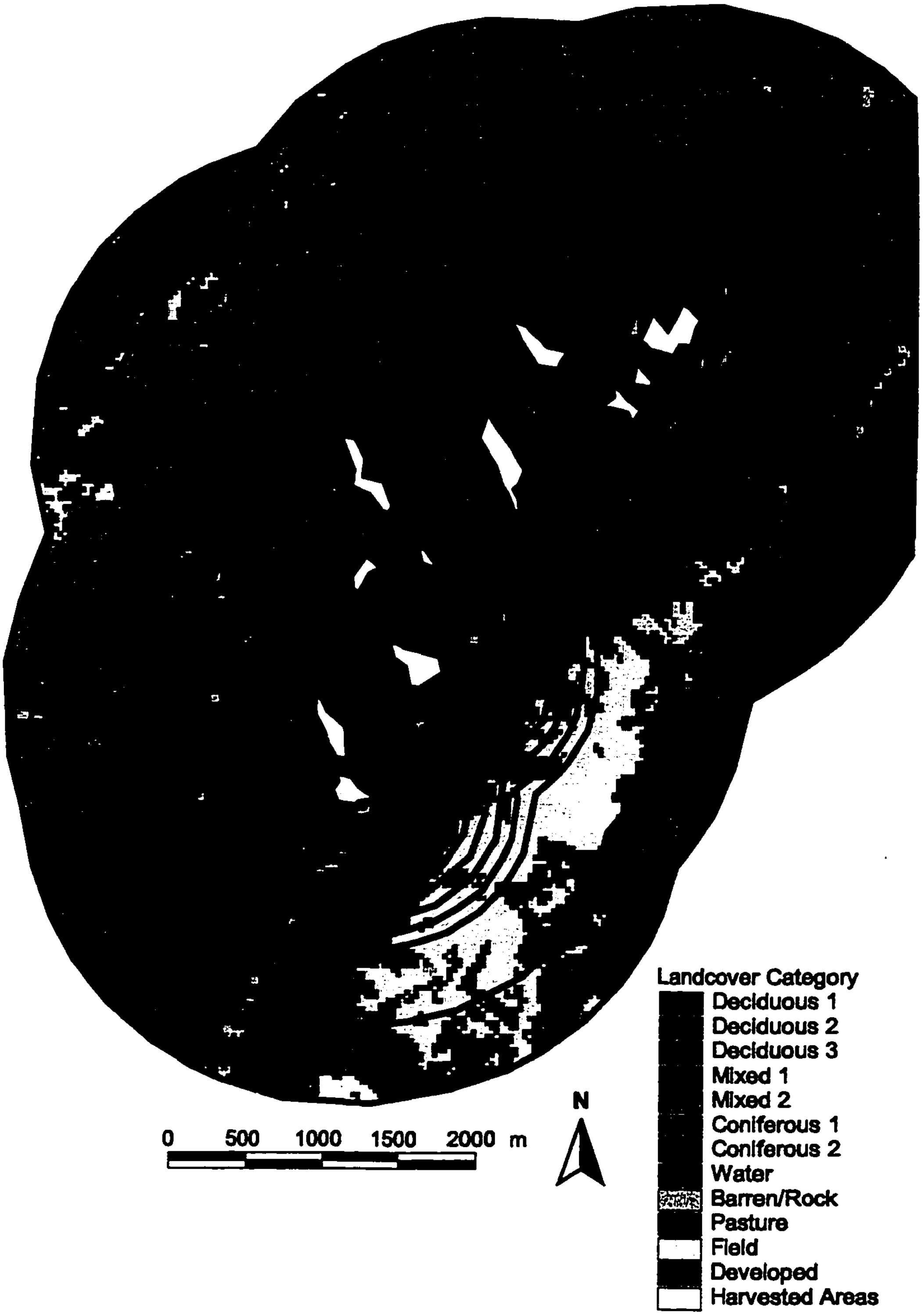
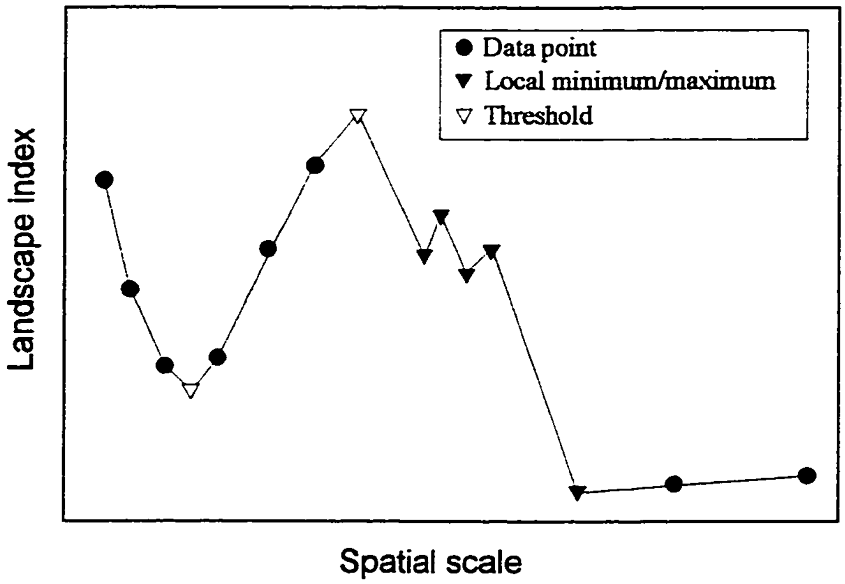

▨ Appalachian Mountains and Valleys
■ Shenandoah National Park
☐ George Washington National Forest
Little Mountain
N
0
50
100
km

Fig. 2

Fig. 3

Fig. 4


0
500
1000
1500
2000
m
N
Landcover Category
Deciduous 1
Deciduous 2
Deciduous 3
Mixed 1
Mixed 2
Coniferous 1
Coniferous 2
Water
Barren/Rock
Pasture
Field
Developed
Harvested Areas


● Data point
▼ Local minimum/maximum
▽ Threshold
Landscape Index
Spatial scale

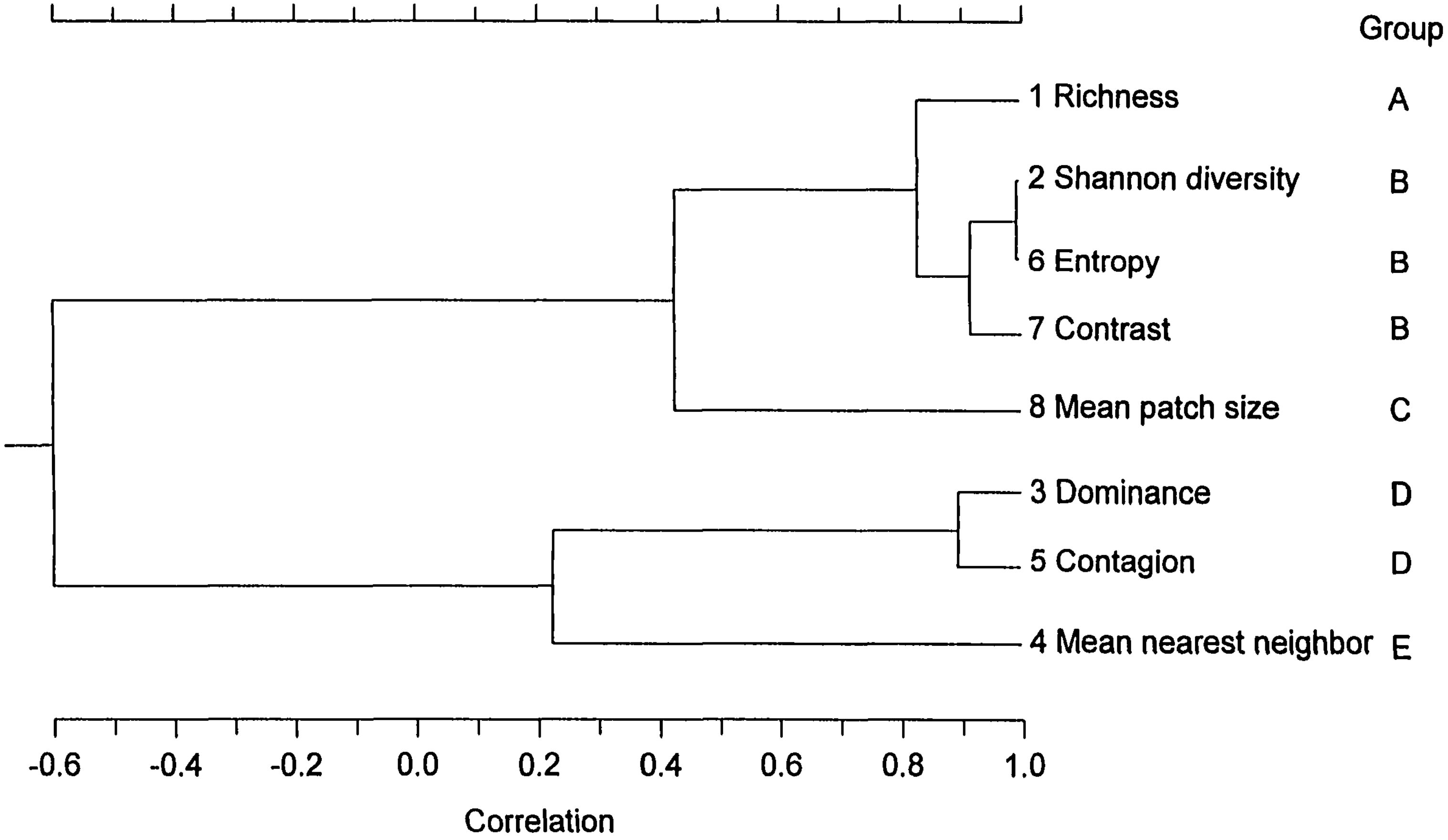

Group
1 Richness
A
2 Shannon diversity
B
6 Entropy
B
7 Contrast
B
8 Mean patch size
C
3 Dominance
D
5 Contagion
D
4 Mean nearest neighbor
E
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0
Correlation

Fig. 6

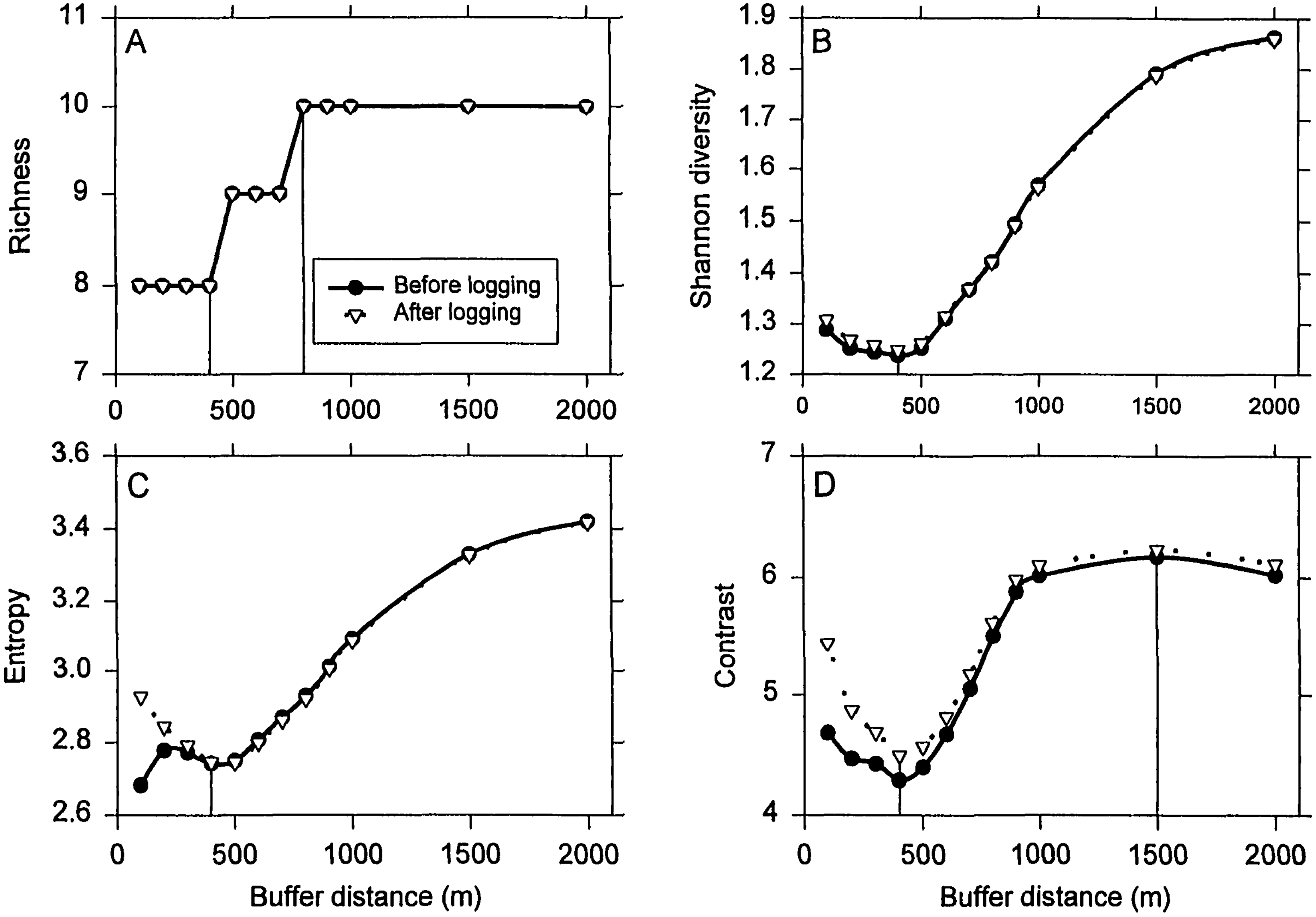

A
Richness
11
10
9
8
7
0
500
1000
1500
2000
Before logging
After logging
B
Shannon diversity
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
0
500
1000
1500
2000
C
Entropy
3.6
3.4
3.2
3.0
2.8
2.6
0
500
1000
1500
2000
Buffer distance (m)
D
Contrast
7
6
5
4
0
500
1000
1500
2000
Buffer distance (m)

Fig. 7

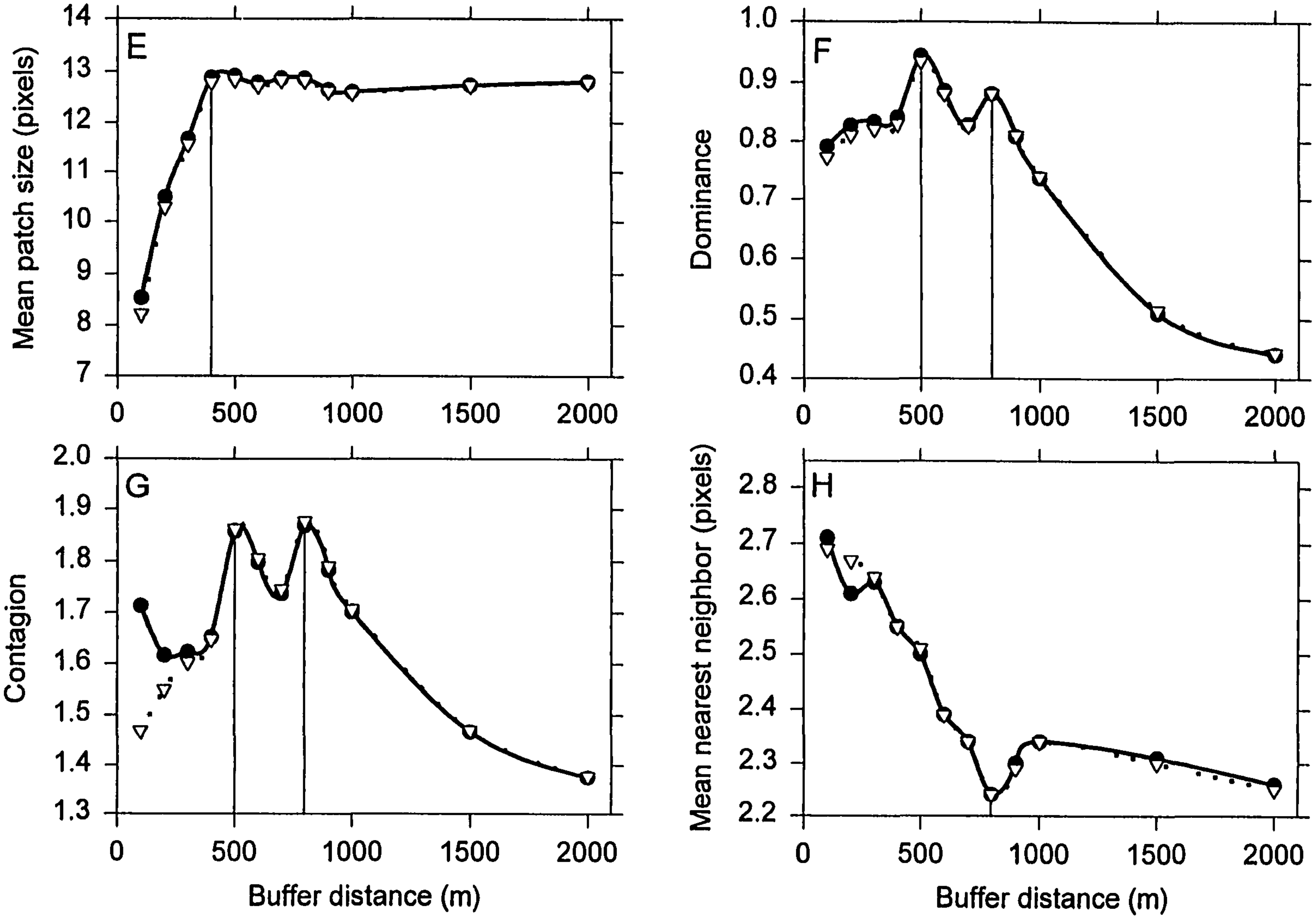


Fig. 7. (Continued)

Fig. 8

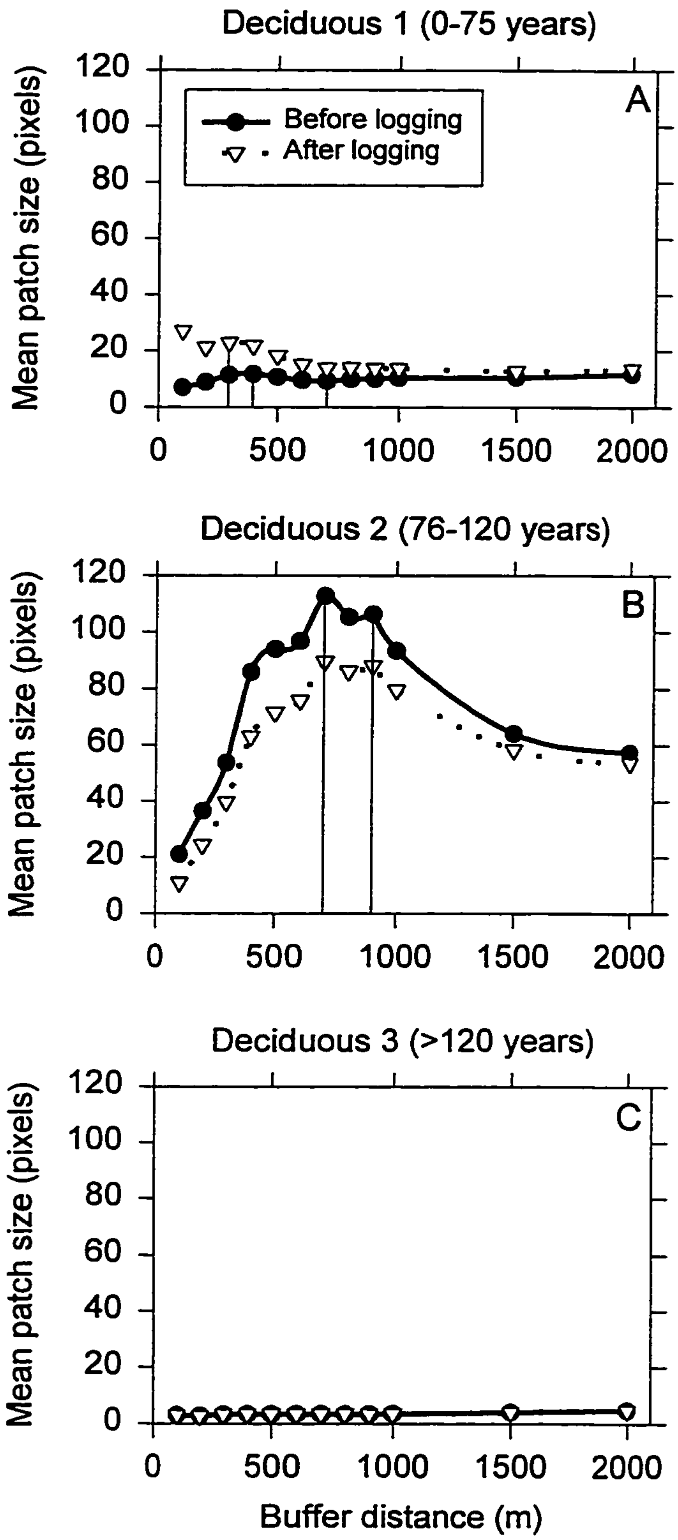

Deciduous 1 (0-75 years)
A
Before logging
After logging
Mean patch size (pixels)
0
20
40
60
80
100
120
0
500
1000
1500
2000
Deciduous 2 (76-120 years)
B
Mean patch size (pixels)
0
20
40
60
80
100
120
0
500
1000
1500
2000
Deciduous 3 (>120 years)
C
Mean patch size (pixels)
0
20
40
60
80
100
120
0
500
1000
1500
2000
Buffer distance (m)

Fig. 9

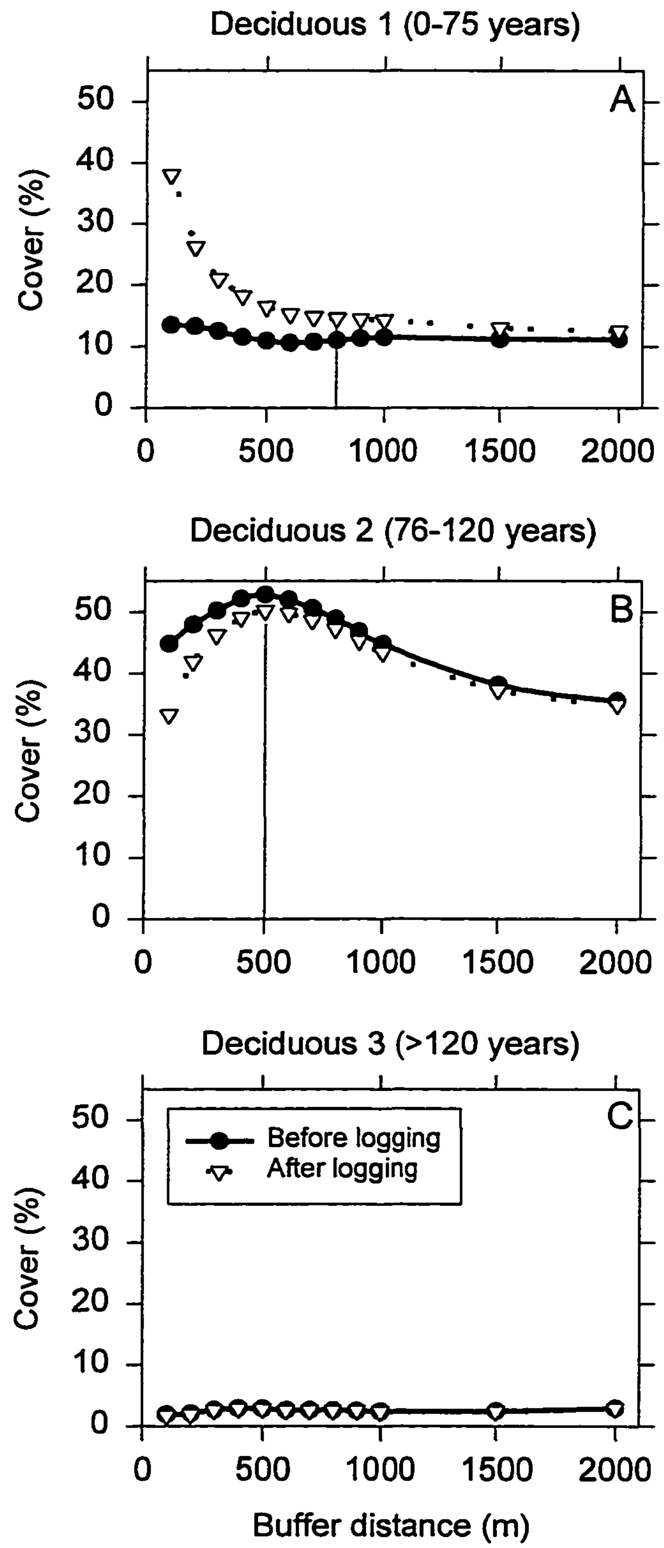
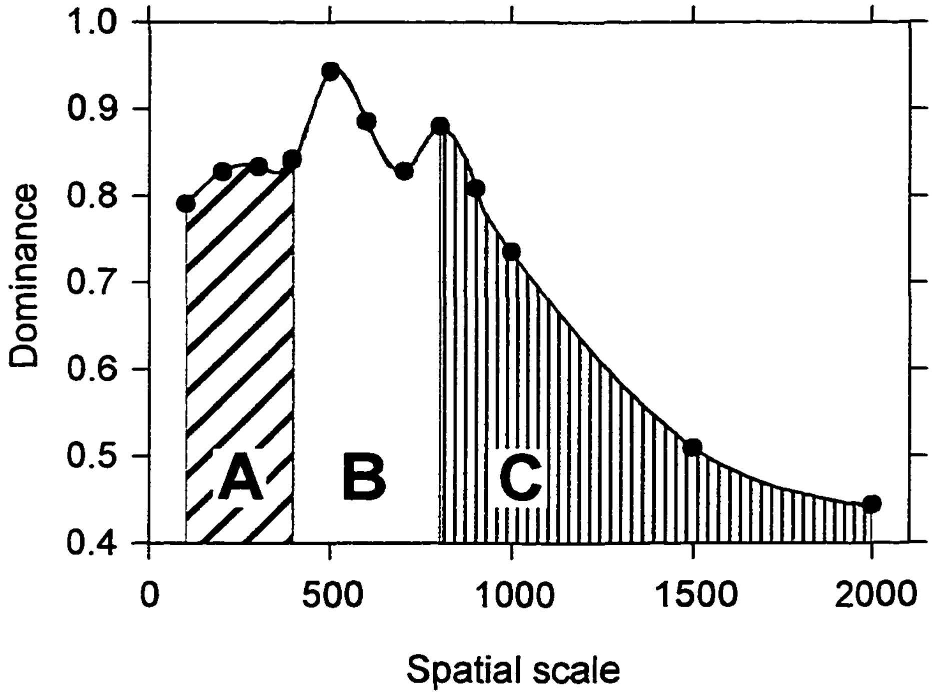

Deciduous 1 (0-75 years)
A
Cover (%)
0
10
20
30
40
50
0
500
1000
1500
2000
Deciduous 2 (76-120 years)
B
Cover (%)
0
10
20
30
40
50
0
500
1000
1500
2000
Deciduous 3 (>120 years)
C
Before logging
After logging
Cover (%)
0
10
20
30
40
50
0
500
1000
1500
2000
Buffer distance (m)

Fig. 10


1.0
0.9
0.8
0.7
0.6
0.5
0.4
Dominance
0
500
1000
1500
2000
Spatial scale
A
B
C

Chapter 4

Running head: Landscape effects on birds and small mammals

Landscape effects of logging on birds and small mammals in managed forest mosaics of the Appalachians

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Abstract.

We studied the effects of logging on small-mammal and bird communities in a managed forest mosaic of the Appalachian Mountains, USA. The landscape was divided into three zones based on the distance from shelterwood cuts (zone 1, inside logged areas; zone 2, 20-400 m from logged areas; zone 3, 1,000-1,500 m from logged areas). We compared landscape characteristics, species presence, and species richness between zones, as well as before and after logging. To determine how changes in the landscape directly influence species presence and richness, we used stepwise regression and discriminant-function analyses. Logging changes species presence and richness in the cut areas, as well as in the surrounding forests. These changes are larger in close proximity of cuts and appear to influence birds more strongly than small mammals. Between 1994 and 1996, presence and richness of bird species changed most in zone 1 and least in zone 3. Presence of the Acadian flycatcher (*Empidonax virescens*), indigo bunting (*Passerina cyanea*), and worm-eating warbler (*Helmitheros vermivorus*) changed significantly between years and zones. The Acadian flycatcher and worm-eating warbler disappeared from cuts, while the indigo bunting increased in presence. Thus, edge-adapted birds replaced forest-interior birds in the cuts. We did not find significant changes for richness of small-mammal species between years and zones. Most changes in presence of small mammals before and after logging cannot be attributed to logging in our study. However, abundances for the white-footed mouse (*Peromyscus leucopus*) increased significantly in zone 1 after logging, while it decreased in zones 2 and 3. We found landscape models that related landscape change to changes in species presence for five species, including the indigo bunting, red-eyed vireo (*Vireo olivaceus*), scarlet tanager (*Piranga olivacea*), worm-eating warbler, and smokey shrew (*Sorex fumeus*). Changes in Shannon diversity and area of young deciduous forest were most important in these models. Shannon diversity also was useful in predicting changes in edge-species richness for birds and abundance of the white-footed mouse. While landscape models were significant, large amounts of variation remained unexplained. Differences in habitat characteristics may sometimes be more important for species and may explain some of the remaining variation. However, we demonstrated that forest species are influenced by changes in the configuration and heterogeneity of the landscape mosaic.

Keywords: landscape structure, forest mosaics, logging, Appalachian forests, small mammals, birds

1. Introduction

Forests of the Appalachian Mountains in the eastern United States have been affected by human settlement and timber harvesting for more than two centuries (Buxton and Gray 1985, Davis 1993, 1996). Because of this complex land-use history and current management practices, little old-growth forest is left (Davis 1993, 1996). The remaining forests are extensive and heterogeneous mosaics with varying compositions of tree species and age classes. A major concern for conservation in the Appalachian Mountains is how continued logging will alter these ecosystems and their native faunas.

Most detailed studies that investigate changes in small-mammal and bird communities after logging have been restricted to either the areas directly affected, or to comparisons of clearcuts with uncut stands in the region (for small mammals, Kirkland 1990; for birds, Webb et al. 1977, Franzreb and Ohmart 1978, Hansson 1983, Derleth et al. 1989, King et al. 1996). Although landscape characteristics may be more important than local habitat conditions in determining the composition and diversity of vertebrate communities (Freemark and Collins 1992, Pearson 1993, Pogue 1998), little is known about how timber extraction impacts vertebrates of the Appalachians at a landscape scale. Much of the current information on the effects of logging at large spatial scales stems from severely fragmented forest systems. Studies in these systems show that forest fragmentation and habitat loss are detrimental to birds and small mammals (Blake and Karr 1987, Robbins et al. 1989, Terborgh 1989, Laurance 1990, Verboom and Van Apeldoorn 1990, Askins et al. 1991). However, predictions derived from fragmentation studies may not apply to Appalachian forests because habitats in these systems are embedded in large forested areas and do not represent isolated habitat islands that are surrounded by large clearcuts or developed land (Angelstam 1986, Welsh and Healy 1993).

To determine how timber extraction affects small-mammal and bird communities in Appalachian forests, we studied the relationship between landscape structure and the presence of small-mammal and bird species at several spatial and temporal scales. We monitored the presence of small mammals and birds (1) within logged areas; (2) within areas in close proximity to logged areas; and (3) within areas greater than 1 km from logged areas. To describe changes in small-mammal and bird distribution as a result of logging, we conducted surveys before and after the forest stands were cut. We hypothesized that: (1) Logging changes the landscape structure of the forest and these changes are more marked within close proximity of the cut areas. (2) After logging, the presence and richness of small-mammal and bird species changes significantly in the landscape, and these changes are most severe in logged areas. (3) Changes in landscape characteristics brought about by logging are directly related to changes in the presence and richness of small-mammal and bird species in the landscape.

2. Methods

2.1. Study area

Our study area is on Little Mountain in the Warm Springs and James River Ranger Districts of George Washington National Forest (GWNF), Virginia (Fig. 1). The GWNF includes a total forest area of 429,705 ha, with portions (36,855 ha) designated as timber management areas (George Washington National Forest 1993). On Little Mountain, federal forests cover an area of 8 km by 4 km, comprising the west-facing slopes with a range of elevation from 600 to 850 m.

Between the fall of 1994 and fall of 1995, 11 areas on Little Mountain, ranging in size from 1.8 to 9.7 ha, were used for shelterwood timber harvest (Fig. 2). In shelterwood harvest, the next stand of trees develops under the partial canopy of trees that are left standing after logging 80 to 85% basal area. The remaining trees usually have a diameter at breast height of 20 cm or more (George Washington National Forest 1993). Shelterwoods rely on natural regeneration, stump sprouts, and seeds stored in the forest duff.

For landscape-ecological studies, we established 85 permanent survey points during the spring and summer of 1994. These points were spread across three landscape zones (Fig. 2): 13 points in the logged area (zone 1); 47 points within 20-400 m from logged areas (zone 2); and 25 points within 1,000-1,500 m from logged areas (zone 3). Survey points were separated by at least 200 m, a distance generally assumed to assure independent sampling during bird surveys (Pendelton 1995). All points were used for landscape analyses and for small-mammal surveys in 1994 and 1996. Bird surveys were conducted at 64 of the permanent points (zone 1, n=12; zone 2, n=32; zone 3, n=20).

We determined the geographic coordinates (±10 m) of each survey point using a global positioning system (GPS) and differentially correcting the data collected in the field with information obtained from a community base station. These positional data were integrated with digital landcover information in a geographic information system

(GIS) and used for landscape analyses. Presence/absence data for birds and small mammals were collected at each survey point in 1994 and 1996.

2.2. Landscape analyses

For landscape analyses, we employed a digital landcover map (Fig. 2) produced from remote-sensing analyses of a Landsat TM satellite image, using techniques described in Leimgruber et al. (1998a). The landcover map accurately delineated successional stages (mature, mid-, and early-successional) of major forest types (deciduous, mixed deciduous-coniferous, and coniferous), as well as logged areas. Previously, we found that this map was particularly useful to assess the effects of forest management at the spatial scale of timber management units (Leimgruber et al. 1998b).

For each survey point we determined the landscape structure by calculating selected indices within a 300-m radius of the points (Fig. 3) using the digital landcover map in FRAGSTATS–a landscape-analysis program available through the Internet (McGarigal and Marks 1995). The following landscape indices were calculated before logging and after logging: mean nearest neighbor distance (MNN), mean patch size (MPS), Shannon diversity (SHDI), contagion (CON), total area for deciduous forest types (mature, mid-, and early-successional; AREAD3, AREAD2, AREAD1, respectively), and mean patch size for deciduous forest types (mature, mid-, and early-successional; MPSD3, MPSD2, MPSD1, respectively; Table 1).

2.3. Bird surveys

We conducted two point counts at each survey point between 1 June and 1 July in 1994 and 1996. Counts lasted for 5 min, and every bird species seen or heard within 50 m of the study point was recorded. We visited each point once in the early morning between 0500 and 0730 h Daylight Savings Time (DST) and once between 0730 and 1000 h. From these data, we determined mean number of points at which a bird species was detected each year for each of the three zones.

2.4. Small-mammal surveys

For small-mammal surveys, we established trap arrays consisting of Sherman (180 mm × 60 mm × 60 mm) live-traps and a cluster of four pitfall traps. We used a stake in the center to mark the survey point and four perimeter stakes, placed 11 m from the center along cardinal directions, to mark a circular area of approximately 400 m^2. All surveys were conducted between 1 July and 3 September in 1994 and 1996. During surveys, two Sherman traps were placed at each perimeter stake and prebaited for three days with rolled oats and sunflower seeds. Following the prebait period, traps were set and checked each morning for five days. Fruit was added to the traps to provide moisture for the animals. The traps that were not shaded by forest trees and shrubs were covered by shingles to reduce the risk of animals overheating. We also placed cotton inside traps to provide animals with sufficient insulation. Captured animals were: (1) examined to determine species identification and gender; (2) weighed; (3) given a unique numbered eartag; (4) examined to determine reproductive condition; and (5) released.

The pitfall array consisted of four containers (diameter, 100 mm; depth, 200 mm) that were arranged with one container in the center and three containers at 1-m distance from the center and separated by 120°. The three peripheral containers were connected to the center trap by drift fences. The containers were dug into the ground and filled one-third with water. We set pitfall traps for eight nights each year between 1 July and 3 September. The array was checked daily. For each captured animal we determined species, gender, and mass.

Presence/absence data for small mammal species at survey points were based on species detected during the five days of live-trapping and the eight days of pitfall-trapping. For the white-footed mouse (*Peromyscus leucopus*), the most common species, we recorded abundances by summing all captures over the trapping period of each year. Recaptures from the same trapping period were omitted from this number.

2.5. Statistical analyses

To test hypothesis 1, that landscape structure changed after logging and that these changes were larger in close proximity of logged areas, we compared mean values for landscape indices between survey points grouped by zones and years. We used a repeated-measures analysis of variance (ANOVA; SYSTAT1996) with zones as the grouping factor and years as the within-group factor.

We also employed a repeated-measures ANOVA to test hypothesis 2 that the presence and richness of small-mammal and bird species changed significantly with logging and that these shifts were larger in logged areas versus those areas away from the logged areas. We compared the mean number of points at which bird and small-mammal species were present, using zones as the grouping factor and years as the within-group factor. All species of small mammals and birds detected at more than 10 points during at least one year of the study were included in this analysis.

To assess changes in species richness, we compared the mean number of species at survey points using the same procedures as for species presence. For birds, separate analyses were conducted to inspect patterns in richness for edge species and for forest-interior species. In this analysis we divided birds into edge species (E), forest-interior species (I), and generalist species (G) based on the investigators' experience and information on life histories of the species (e.g. Ehrlich et al. 1988, DeGraaf and Rappole 1995).

For the testing of hypothesis 3–that alterations in landscape structure through logging also changed the presence and richness of small-mammal and bird species at the landscape scale–we used a combination of stepwise discriminant and multiple-regression techniques. First, we determined a relative-change index for each landscape index by dividing the value from 1996 by that from 1994. To avoid divisions by zero, we transformed the data by adding 0.01 to each value prior to the calculation of the relative change index. No landscape index remained constant between 1994 and 1996; increases in the value for a landscape index between the years resulted in a change index >1, and decreases resulted in a change index <1. Second, we determined relative changes in the presence of a species by classifying survey points into three groups based on presence/absence patterns. Group 1 included points at which a species was detected in

1994, but not in 1996. These points provided information on which changes in landscape structure might negatively affect the presence of a species. Group 2 comprised all points at which a species was present in 1996 irrespective of whether the species was found in 1994. Survey points in group 2 were used to determine which changes in landscape structure did not have an effect or had a positive effect on the presence of a species. Group 3 contained all of the remaining points (i.e. those at which the species was not detected in 1994 and 1996). Because we could not infer why points in group 3 were not utilized, these points were omitted from further analysis. We used stepwise discriminant-function analysis with backward selection of variables to identify the combination of landscape-change indices that differentiated best between the points in groups 1 and 2. We retained only variables that had F-values ≥ 4.00. This procedure allowed us to determine how relative changes in landscape indices can be combined into linear functions that best predict changes in the presence of a species.

To evaluate how the relative change in landscape structure influenced species richness of all species of birds, edge species, forest-interior species, and small mammals, we also calculated a change index for these vertebrate-community variables following the same procedures as used to calculate a change index for landscape indices. Stepwise multiple regression with backward selection of variables was employed to determine the best predictors for changes in species richness. Again, we retained only variables that had $\underline{F}$-values ≥ 4.0.

3. Results

3.1. Changes in landscape indices

Several landscape indices showed significant differences among zones and between years (Table 2 and 3). Significant changes between 1994 and 1996 can be attributed to logging and were detected for five landscape indices: SHDI, AREAD1, AREAD2, AREAD3, and MPSD1 (Table 2 and 3). Of these, SHDI, AREAD1 and AREAD3 had significant F-values for the interaction term year × zone, demonstrating that these indices changed more in some zones than others. SHDI increased in zone 1, but changed little in zones 2 and 3 (Table 2). AREAD1 increased markedly in zone 1, moderately in zone 2, and little in zone 3 (Table 2). AREAD3 decreased more in zone 1 than in zones 2 and 3 (Table 2).

MPS, CON, and MPSD1 were significantly different between zones, but MPS and CON did not change between years (Table 2 and 3). Differences between zones probably can be attributed to the increasing influence of surrounding agricultural lands on the landscape structure (Fig. 3).

3.2. Changes in birds

We detected 44 species of birds in our study region (Table 4). Before logging, we counted 40 species; this number dropped to 29 after forest stands were cut (Table 4). The mean species richness declined significantly between 1994 and 1996, but we did not detect significant differences in species richness among zones (Table 5). The slopes for the decline of mean species richness in the three zones were not significantly different as indicated by a low F-value of the interaction term year × zone. These patterns were similar for mean species richness of interior species (Table 5). Mean species richness for edge species also did not change significantly with time (Table 5), but increased in zone 1 and declined in zones 2 and 3 (Fig. 4C). The F-value for the interaction term in the last comparison was significant with a P of 0.058. Plots of mean species richness indicate that interior species declined in zone 1 and were replaced by an increasing number of edge species (Fig. 4B, C).

For statistical analyses on changes in presence of birds, we used 10 species that were found at more than 10 survey points during at least one year (Table 5). The total number of points at which the Acadian flycatcher, American goldfinch, downy woodpecker, tufted titmouse, indigo bunting, red-eyed vireo, eastern towhee, and scarlet tanager were present decreased between 1994 and 1996. During the same period, presence increased for the pine warbler and worm-eating warbler (Table 4). The mean number of points at which species were present declined significantly for the Acadian flycatcher, American goldfinch, tufted titmouse, red-eyed vireo, eastern towhee, and scarlet tanager, while it increased significantly for worm-eating warbler (Table 5). The increase in the mean number of points for the pine warbler was not significant (Table 5).

Significant F-values for the interaction term year × zone indicate that presence changed differently among zones and across years for the Acadian flycatcher, indigo bunting, and worm-eating warbler (Table 5). Some of these patterns resulted primarily from changes in zone 1, the logged area (Fig. 5). The Acadian flycatcher disappeared from zone 1 after logging and declined markedly in zone 2 (Fig. 5A). The indigo bunting increased in zone 1 in 1996 and declined in zone 2 (Fig. 5B). Both species did not change conspicuously in zone 3. The worm-eating warbler increased in zones 2 and 3 after the logging and disappeared from zone 1 (Fig. 5C).

3.3. Changes in small mammals

During 1994 and 1996 we detected 13 species of small mammals at survey points (Table 7), the most common being the white-footed mouse, followed by the eastern chipmunk, northern short-tailed shrew, and smokey shrew. Shrews generally declined during the study and the eastern chipmunk showed an increase in presence after logging occurred (Table 6). However, mean species richness did not decline significantly between years and also was not different among zones (Table 7). Statistical analysis on the presence of small-mammals was restricted to the three species present at more than 10 survey points: smokey shrew, northern short-tailed shrew, and eastern chipmunk (Table 6).

We did not find significant differences in presence between years or among points for the smokey shrew (Table 7). Presence significantly declined for northern short-tailed shrew and increased for eastern chipmunk, but these changes did not differ in slope among zones, and there is no significant evidence that short-tailed shrews or eastern chipmunks were affected by logging (Table 7). When comparing mean abundance of white-footed mice among zones and between years in a repeated-measures ANOVA, we found that abundance changes between years differed among zones (Fig. 6). In the logged areas (zone1), the white-footed mouse increased in abundance, while it declined in zones 2 and 3 (Fig. 6).

3.4. Effects of landscape changes on diversity and presence of species

Using discriminant-function analysis, we found landscape models that predicted changes in species presence based on changes in landscape indices for five species (Table 9). All models were based on combinations of indices for five landscape measures: SHDI, CON, AREAD1, MPS, and MPSD1 (Table 8). Mean values for changes in these indices demonstrate that AREAD1and MPSD1 increased between years and were at average greater than one. SHDI had an index average only slightly larger than one, indicating that values for SHDI increased little. However, we showed earlier that SHDI increased more in close proximity to logged areas than at greater distances. Although CON and MPS differed among zones, these indices had an index average of 1 and changed little between years.

Four of the five species had landscape change models with significant F-values for the overall model (Table 9). The presence/absence of the indigo bunting is best predicted by changes in SHDI. This species remained or newly appeared at points that had large increases in SHDI of landcover types (Table 9). MPS, SHDI, and CON had change indices that best predicted the presence/absence of scarlet tanagers (Table 9). Increases in SHDI had the greatest influence in the model for the scarlet tanager, as implied by its large partial F-value (Table 9). The presence/absence values for the worm-eating warblers and smokey shrews were best predicted by increases in AREAD1 (Table 9). AREAD1 and MPSD1 were the best predictors for the presence/absence of the red-eyed vireo (Table 9). While increases in area were positively correlated with the discriminant axis, MPSD1 had a negative coefficient. Because partial F-values for these two change variables are only slightly different, they cancel each other out and, as a result the overall model for the red-eyed vireo is not significant. This suggests that the red-eyed vireo is positively associated with increases in early-successional habitats, but that it does not select for large patches of this habitat type. We did not find significant models that related landscape change to presence/absence for the Acadian flycatcher, American goldfinch, downy woodpecker, pine warbler, tufted titmouse, eastern towhee, northern short-tailed shrew, and eastern chipmunk.

Results from stepwise regression analyses demonstrated that changes in richness were positively correlated with changes in mean nearest neighbor distance. Changes in edge-species richness were positively correlated with changes in SHDI and negatively correlated with changes in MPSD3. Changes for SHDI averaged >1, while those in MPSD3 averaged <1 (Table 8). The smaller the average change in MPSD3, the larger the loss of this habitat type between 1994 and 1996. Thus, the landscape model demonstrates that edge species tend to increase with an increase in heterogeneity, as expressed in SHDI, and a loss of mature deciduous forests (MPSD3). While the $\underline{F}$-values for the richness landscape models were significant, the $\underline{r}^2$-values are low. SHDI has the highest partial $\underline{r}^2$-value, stressing its importance in explaining changes in richness. We did not find significant landscape models for richness of forest-interior birds or of small mammals. Changes in abundance of the white-footed mouse also was positively correlated with increases in SHDI, but again the $\underline{r}^2$-value for this relationship was low.

4. Discussion

The detrimental effects of habitat loss and fragmentation on biodiversity in forested ecosystems are well documented and have become a major area of study in conservation biology during the past decades (e.g. Blake and Karr 1987, Terborgh 1989, Robbins et al. 1989, Laurance 1990, Verboom and Van Apeldoorn 1990, Askins et al. 1991, Saunders et al. 1991) . However, forested ecosystems in the eastern United States often are not fragmented systems, but rather are heterogeneous mosaics of forest stands in different successional stages. Recent studies have put emphasis on studying changes in clearcuts and in adjacent areas (King et al. 1996); they treat clearcuts as distinct islands patches in a sea of forest. We believe that this approach still restricts our ability to understand some of the processes occurring in managed forest mosaics. Many forest species are not confined to specific forest patch types (Pearson 1993, Pogue 1998). The distribution of vertebrate organisms in a forest-mosaic system may be less regulated by area and edge effects than by other landscape characteristics, such as patch diversity, heterogeneity, spatial arrangement of patches, or mean patch size. Additionally, no study to date has shown an association between relative changes in the forest landscape structure and changes in the vertebrate communities.

Logging altered the landscape structure of the forest mosaic in our study region at different spatial scales, and these alterations were most marked in close proximity to the harvested forest stands (Leimgruber et al. 1998b). The richness and presence of bird species, as well as the abundance of the white-footed mouse, showed similar patterns, with the largest changes occurring in close proximity to the cut areas. Generally, changes in presence and richness were more pronounced for birds than in small mammals, suggesting that birds may be better indicator species for the detection of changes in vertebrate communities brought about by logging in forest mosaics.

4.1. Local effects of logging

For birds, the detailed analyses of the richness and presence patterns at different distances from the cut areas demonstrate–not surprisingly–that logging had a pronounced impact. At the local scale of the cut, there were shifts in richness and presence from forest-interior species to edge species. The richness of forest-interior birds declined, while that of edge species increased. Similar patterns were found for the presence of forest-interior species (Acadian flycatcher and worm-eating warbler) and an edge species (indigo bunting). This supports the general notion that logging has adverse effects through habitat loss and edge effects for forest-interior species, while edge-adapted species respond positively to disturbance with an increase in richness and abundance (Freemark and Merriam 1986). However, some of the decline in species richness and presence of birds in our study may reflect annual variation. Richness declined similarly in other forest habitats of the region that were not intensively managed. For example, at the nearby Gathwright Wildlife Refuge, mean species richness for birds declined from 5.90 in 1995 to 4.15 in 1996 (F=13.57, P<0.01; Leimgruber, unpubl. data).

Small mammals were little affected by logging at the local scale. Our data suggests that only the white-footed mouse responded directly to shelterwood cutting and increased in abundance in the cut areas. This is consistent with other studies that have demonstrated increases in abundance of rodents due to increases in the availability of shelter and seeds in shelterwood cuttings, as well as in clearcuts (Kirkland 1990, Von Trebbra et al. 1998).

Results from previous studies of logging on small-mammal communities also suggest that eastern chipmunks and smokey shrews usually increase, while northern short-tailed shrews decline (Kirkland 1977, 1990). We did not find conclusive evidence that supports these suppositions. Eastern chipmunks increased between the years, but these increases did not differ between shelterwood cuts and the forest areas away from the cuts. Smokey shrews showed no significant changes between years or among zones. The presence of the northern short-tailed shrew decreased over the course of our study, but again there were no significant differences among zones. Other work suggests that the distribution of many small mammals in forest mosaics may be more linked to habitat (Morris 1987, Carey and Johnson 1995) and microhabitat factors (Dueser and Shugart 1979) than to landscape features. For example, the northern short-tailed shrew is reported to have a narrow niche (Dueser and Shugart 1979) and to depend on soil moisture (Owen 1994). If soil moisture varies between years due to differences in precipitation, one would expect general declines that would be independent of changes in landscape characteristics.

4.2. Landscape effects of logging

Our results for presence and richness of vertebrates in different zones demonstrate that logging influences vertebrate distribution in the surrounding landscape. As hypothesized, these effects declined with distance from the cut areas and appeared to be important up to about 400 m from the edge of the shelterwood cuts.

For species with relatively large sample sizes, we demonstrated that changes in landscape structure were correlated with changes in the presence and richness of species. Logging affects vertebrate communities not just in the cut areas, but also in the surrounding areas through changes in the spatial configuration and heterogeneity of the landscape. Landscape indices that changed most with logging, such as SHDI or AREAD1, also were most important in explaining fluctuations in species richness and presence.

For birds, the relationship of richness of edge species to SHDI and MPSD3 may reflect this group's preference for habitats that are increasingly heterogeneous and that contain only small patches of mature deciduous forests. This conclusion is further strengthened by the fact that patterns in presence of indigo buntings were positively correlated with SHDI. Shannon diversity (SHDI) is a measure of habitat heterogeneity; it increases as the number of different patch types increases and as the proportion of area covered by the different patch types approach equality (McGarigal and Marks 1995). Indigo buntings did not decline between the years, but shifted in presence from zones 2 and 3 into zone 1, the latter being the zone in which SHDI increased the most. This is consistent with the fact that indigo buntings prefer woodland clearings, forest edges, and open woodlands (i.e. patch types that are frequently found in heterogenous mosaics of heavily managed forests; Payne 1992, DeGraaf and Rappole 1995).

Scarlet tanagers declined drastically between the years. However, landscape analyses show that points at which this species occurred in 1996 had increased in MPS and SHDI, and had decreased in CON. This forest-interior species typically is found in heterogeneous habitats, but may avoid disturbance by logging.

The worm-eating warbler, another forest-interior species, disappeared from logged areas in 1996, but increased in the other two zones. In the landscape analysis, the presence of this species showed a positive association with increases in AREAD1. Worm-eating warblers avoid cuts and disturbed areas, but shift to other areas in the landscape that are in close proximity to disturbed stands. It prefers extensively forested areas with dense undergrowth (DeGraaf and Rappole 1995). On the landscape scale, worm-eating warblers may be positively affected by increased cover along the margins of cuts in extensively wooded areas. Such a preference would explain their positive association with overall increases in the amount of early-successional habitats.

The red-eyed vireo is a generalist forest species. It declined between years, but these declines were not different among zones. However, the results from the landscape analyses provide evidence that this species responds positively to the increase in early-successional habitats as long as these forests are found in small patches. Red-eyed vireos often nest in relatively low trees and bushes (2-3 m) with dense foliage, but can also be found in areas with large trees and little understory in mixed mesophytic forests (DeGraaf and Rappole 1995).

We did not find a significant landscape model for interior species richness or for the presence of a number of bird species, including the Acadian flycatcher, American goldfinch, downy woodpecker, pine warbler, tuffted titmouse, and eastern towhee. Only the Acadian flycatcher showed significant changes in presence between the years that can be attributed to logging. The pattern of presence/absence across zones for this species indicate that it is not only affected in the logged areas, but also in the surrounding landscape. The absence of a landscape model for Acadian flycatchers is due to this species declining so sharply that data were insufficient for analysis. Some of the other species, such as eastern towhee and tuffted titmouse, may simply be affected by landscape characteristics at a larger scale. Our field surveys were restricted entirely to the interior portion of the forests on Little Mountain. Other landscape-ecological studies have suggested that the presence of some bird species is more strongly associated with habitat and microhabitat factors than with landscape characteristics (Pearson 1993, Pogue 1998).

Fluctuations among survey points in species richness of small-mammal species, as well as in the presence of the northern short-tailed shrew and the eastern chipmunk, were not related to landscape change. Although smokey shrews did not decline significantly between years and their presence patterns were not different among zones, we found that changes at points where the species was detected were related to increases in the amount of early-successional forest. The relationship between increases of Shannon diversity and the presence for white-footed mouse is best explained by this species' preference for diverse and heterogenous forest habitats. Presence of many of the small mammals in our forest region may be strongly correlated with habitat and microhabitat features, such as availability of shelter, presence of dead logs, amount of leaf litter, and food resources.

4.3. Cuts or mosaics?

We demonstrated in this and a previous study (Leimgruber et al. 1998b) that logging changes the landscape structure and that such effects are greater close to the cuts. The influence of logging on the landscape structure and how far such effects extend into the surrounding landscape depends on several factors, including: the heterogeneity in the landscape before logging; the size, number and dispersion of the logged areas; and the scale at which the phenomena are studied. Previously, we demonstrated that some scales are more important than others and that thresholds can be used to define the scales at which the influence of logging is best studied (Leimgruber et al. 1998b). We also showed that the most important scale includes all areas that are within 400 m of the management units (Leimgruber et al. 1998). The results of our bird and small-mammal surveys support the findings from these previous studies. The effects of logging on birds and small mammals were most important in zones 1 and 2 that is, at distances less than 1,000 m from the logged forest stands.

Landscape models for some species and for richness were significant, but $\underline{r}^2$-value were low, indicating that most variation remained unexplained. Previous research on the importance of landscape and local habitat characteristics shows that habitat features are sometimes more important than landscape characteristics (Pearson 1993, Pogue 1998). Another possible explanation for the lack of strong species-landscape models in our study region may be found in the land use history of our study region. All areas were used extensively for timber harvest in the past 150 years. Species that are sensitive to disturbance on a habitat and landscape scale may have disappeared early, and most remaining species may be resilient. However, we did show that changes in the landscape can explain changes in numbers and presence/absence of vertebrate species, especially birds. Our research also demonstrates that species do not live in patches of old or cut forest, but in mosaics of stands and that the spatial configuration and heterogeneity of these forests is what counts.

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Table 1. Abbreviations (in parentheses), descriptions, and equations for landscape indices used in analyses (adapted from McGarigal and Marks 1995).

Landscape metric	Description	Formula[a]
Mean nearest neighbor distance (MNN)	Mean of all Euclidean distances between patches. Distance calculated from edge to edge between nearest patches of same type.	
Shannon diversity (SHDI)	Relative measure of diversity in patch types based on frequency and eveness of cells of each patch type present in sampling area.	$SD = -\sum_{i=1}^{m} p_i \cdot \ln(p_i)$
Contagion (CON)	Quantifies degree of clumping within sampling area.	$CON = 2 \cdot \ln(m) - ENT$
Area deciduous forest (AREA)	Expresses area (ha) covered by different successional forest categories. Calculated for early-successional (AREAD1), midsuccessional (AREAD2), and mature (AREAD3).	
Mean patch size (MPS)	Mean area (ha) of patches. Calculated for patches of all types and for deciduous-forest patches of early-succesional (MPSD1), midsuccessional (MPSD2), and mature (MPSD3) types.	

[a] Equation symbols: p_i, fraction of sampling area occupied by attribute i; m, number of attributes in sampling area; ENT, entropy ($ENT = -\sum_{i=1}^{m} \sum_{j=1}^{m} p_{ij} \cdot \ln(p_{ij})$); p_{ij}, number of times that attributes i and j are adjacent when examined in a moving window of 3 × 3 cells.

Table 2. Means and standard errors for landscape indices.

	1994			1996		
Landscape index	Zone 1	Zone 2	Zone 3	Zone 1	Zone 2	Zone 3
Mean nearest neighbor (MNN)	69.02±4.58	67.78±2.44	68.34±3.30	69.38±4.77	68.29±2.54	68.34±3.44
Shannon diversity (SHDI)	1.26±0.06	1.32±0.03	1.49±0.04	1.34±0.06	1.34±0.03	1.49±0.04
Contagion (CON)	39.73±2.53	37.08±1.35	31.94±1.83	38.73±2.45	36.91±1.30	31.94±1.77
Area deciduous forest						
Early-successional (AREAD1)	3.37±1.00	4.33±0.53	3.61±0.72	8.18±1.12	6.40±0.59	4.18±0.80
Midsuccessional (AREAD2)	14.61±0.98	13.27±0.52	12.62±0.71	11.06±0.97	12.38±0.52	12.36±0.70
Mature (AREAD3)	0.87±0.16	0.63±0.08	0.61±0.11	0.42±0.12	0.51±0.07	0.70±0.09
Mean patch size						
All patch types (MPS)	0.92±0.06	0.92±0.03	0.77±0.04	0.93±0.06	0.93±0.03	0.77±0.04
Early-successional (MSPSD1)	0.70±0.61	1.81±0.32	0.84±0.44	2.88±0.89	3.53±0.47	0.99±0.64
Midsuccessional (MPSD2)	4.41±1.23	4.12±0.66	4.27±0.89	1.86±1.13	3.58±0.60	4.11±0.81
Mature (MPSD3)	0.25±0.03	0.19±0.02	0.25±0.02	0.20±0.03	0.18±0.02	0.26±0.02

Table 3. Effects of zone and year on changes in landscape indices. *F*-values given for group factor (zone), within-group factor (year), and interaction term (year × zone). Significance levels: *, *P*≤0.05; **, *P*≤0.01; ***, *P*≤0.001.

	F-value		
Landscape index	Zone	Year	Interaction
Mean nearest neighbor distance (MNN)	0.025	0.169	0.065
Shannon diversity (SHDI)	6.134**	13.722***	5.298**
Contagion (CON)	3.727*	1.743	0.814
Area deciduous forest			
Early-successional (AREAD1)	2.383	19.059***	3.677*
Midsuccessional (AREAD2)	0.133	8.174**	2.500
Mature (AREAD3)	0.458	4.407*	3.168*
Mean patch size			
All patch types (MPS)	5.198**	0.774	0.792
Early-successional (MPSD1)	5.865**	9.229***	1.987
Midsuccessional (MPSD2)	0.550	3.703	1.556
Mature (MPSD3)	2.199	2.295	1.009

Table 4. Number of points at which bird detected on Little Mountain. Type refers to classification as edge (E), generalist (G), or interior (I) species.

		No. points	
Species	Type	1994	1996
Yellow-billed cuckoo (*Coccyzus americanus*)	G	1	0
Ruby-throated hummingbird (*Archilochus colubris)*	E	2	0
Red-headed woodpecker (*Melanerpes erythrocephalus*)	G	1	0
Red-bellied woodpecker (*M. carolinus*)	G	1	0
Downy woodpecker (*Picoides pubescens*)	G	13	1
Hairy woodpecker (*P. villosus*)	I	1	1
Northern flicker (*Colaptes auratus*)	G	1	0
Pileated woodpecker (*Dryocopus pileatus*)	I	8	3
Eastern wood-pewee (*Contopus virens*)	G	2	3
Acadian flycatcher (*Empidonax virescens*)	I	13	3
Least flycatcher (*E. minimus*)	G	1	0
Great crested flycatcher (*Myiarchus crinitus*)	G	2	5
Yellow-throated vireo (*Vireo flavifrons*)	G	1	0
Blue-headed vireo (*V. solitarius*)	G	4	0
Red-eyed vireo (*V. olivaceus*)	G	41	28
Blue jay (*Cyanocitta cristata*)	G	3	0
Carolina chikadee (*Poecile carolinensis*)	G	8	0
Black-capped chickadee (*P. atricapillus*)	G	1	2
Tufted titmouse (*Baeolophus bicolor*)	G	20	6
White-breasted nuthatch (*Sitta carolinensis*)	I	8	2
Carolina wren (*Thryothorus ludovicianus*)	G	1	0

Table 4. (Continued)

Species	Type	No. points 1994	No. points 1996
Blue-gray gnatcatcher (*Polioptila caerulea*)	G	8	9
Wood thrush (*Hylocichla mustelina*)	G	2	2
Golden-winged warbler (*Vermivora chrysoptera*)	G	0	1
Northern parula (*Parula americana*)	G	0	1
Yellow warbler (*Dendroica petechia*)	G	1	0
Chestnut-sided warbler (*D. pensylvanica*)	G	4	0
Pine warbler (*D. pinus*)	I	5	15
Prairie warbler (*D. discolor*)	E	5	1
Cerulean warbler (*D. cerulea*)	I	0	1
Black-and-white warbler (*Mniotilta varia*)	I	1	1
American redstart (*Setophaga ruticilla*)	E	1	7
Worm-eating warbler (*Helmitheros vermivorus*)	I	7	31
Ovenbird (*Seiurus aurocapillus*)	I	7	4
Kentucky warbler (*Oporornis formosus*)	I	0	1
Hooded warbler (*Wilsonia citrina*)	I	3	0
Scarlet tanager (*Piranga olivacea*)	I	22	7
Eastern towhee (*Pipilo erythrophthalmus*)	G	21	7
Chipping sparrow (*Spizella passerina*)	E	7	1
Northern cardinal (*Cardinalis cardinalis*)	E	3	1
Rose-breasted grosbeak (*Pheucticus ludovicianus*)	G	5	0
Indigo bunting (*Passerina cyanea*)	E	23	22
Brown-headed cowbird (*Molothrus ater*)	E	4	6
American goldfinch (*Carduelis tristis*)	E	19	3

Table 5. Mean species richness and mean number of points at which common birds were detected. F-values given for group factor (zone), within-group factor (year), and interaction term (year × zone). Significance levels: *, P≤0.05; **, P≤0.01; ***, P≤0.001.

	$\bar{x}$±SE		F-value		
	1994	1996	Zone	Year	Interaction
Mean species richness	4.323±0.298	2.062±0.178	1.56	39.28***	0.51
For interior species	1.154±0.139	0.369±0.068	0.50	23.55***	0.48
For edge species	0.985±0.123	0.554±0.096	0.97	3.23	2.98
Acadian flycatcher	0.200±0.050	0.046±0.026	2.51	17.17***	7.09**
American goldfinch	0.292±0.057	0.046±0.026	0.25	13.08***	0.62
Downy woodpecker	0.200±0.050	0.015±0.015	0.22	8.69**	0.56
Tufted titmouse	0.308±0.058	0.062±0.030	0.56	11.56**	0.00
Indigo bunting	0.354±0.060	0.292±0.057	3.44*	0.17	4.51*
Pine warbler	0.077±0.033	0.169±0.047	0.97	1.56	2.23
Red-eyed vireo	0.631±0.060	0.385±0.061	0.18	6.01**	2.29
Eastern towhee	0.323 ±0.058	0.092±0.036	1.98	10.76**	1.07
Scarlet tanager	0.338±0.059	0.077±0.033	0.19	8.86**	1.94
Worm-eating warbler	0.108±0.039	0.323±0.058	2.28	5.70*	3.54*

Table 6. Number of points at which mammal species detected on Little Mountain.

	No. points	
Species	1994	1996
Masked shrew (*Sorex cinereus*)	7	1
Long-tailed shrew (*S. dispar*)	1	0
Smoky shrew (*S. fumeus*)	12	8
Pygmy shrew (*S. hoyi*)	6	3
Northern short-tailed shrew (*Blarina brevicauda*)	18	9
Eastern chipmunk (*Tamias striatus*)	8	27
White-footed mouse (*Peromyscus leucopus*)	85	84
Deer mouse (*P. maniculatis*)	7	1
Golden mouse (*Ochrotomys nutalli*)	3	5
Eastern woodrat (*Neotoma floridana*)	1	0
Southern red-backed vole (*Clethrionomys gapperi*)	1	2
Meadow vole (*Microtus pennsylvanicus*)	0	1
Woodland jumping mouse (*Napaeozapus insignis*)	4	1

Table 7. Mean species richness and mean number of points at which common small mammals were detected. F-values given for group factor (zone), within-group factor (year), and interaction term (year × zone). Significance levels: *, $P \leq 0.05$; **, $P \leq 0.01$; ***, $P \leq 0.001$.

	Mean		F-value		
	1994	1996	Zone	Year	Interaction
Richness	1.824	1.671	1.87	2.08	0.44
Smokey shrew	0.141	0.094	1.41	2.85	1.46
Northern short-tailed shrew	0.212	0.106	0.78	4.79*	1.56
Eastern chipmunk	0.094	0.318	2.99	9.59**	0.68

Table 8. Mean and standard error of landscape change variables that were included in landscape models for species presence and richness.

Landscape index	Change index ($\bar{x}$±SE)
Mean nearest neighbor (MNN)	1.01±0.01
Shannon diversity (SHDI)	1.02±0.01
Contagion (CON)	1.00±0.01
Area deciduous forest	
Early-successional (AREAD1)	95.46±91.35
Mean patch size	
All patch types (MPS)	1.01±0.01
Early-successional (MPSD1)	6.71±1.97
Mature (MPSD3)	0.93±0.06

Table 9. Landscape change models from discriminant analysis using changes in landscape variables to predict changes in presence of birds and small mammals. Group 1 contains survey points at which species present in 1994, but not in 1996. Group 2 contains all points at which species present in 1996. Significance levels for overall F-values: *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

Group 1	 2	Landscape-change model[a]	Partial F	Overall F	Canonical correlation
		Indigo bunting			
16	19	+ 1.00 SD^{rel}	12.00	12.00**	0.52
		Red-eyed vireo			
23	25	+ 2.42 $AREAD1^{rel}$	5.08	2.54	0.32
		- 2.2 $MPSD1^{rel}$	4.08		
		Scarlet tanager			
21	4	+ 1.11 MPS^{rel}	8.64	5.00**	0.65
		+ 1.65 SD^{rel}	13.26		
		+ 1.06 CON^{rel}	5.86		
		Worm-eating warbler			
2	20	+ 0.08 $AREAD1^{rel}$	18.25	18.25***	0.69
		Smokey shrew			
10	8	+ 1.00 $AREAD1^{rel}$	4.75	4.75*	0.48

[a] Abbreviations for landscape indices as in Table 1. For these analyses, relative change in variable calculated as $X^{rel}=X_{1996}/X_{1994}$.

Table 10. Landscape models using stepwise regression analyses to determine which landscape changes best predict changes in species richness of birds and in abundance of white-footed mice. Significance levels of F-values: *, $P<0.1$.

Landscape model[a]	Partial r^2	Model r^2	F-value
Relative richness of bird species			
+ 1.40 MNN^{rel}	0.08	0.08	5.51*
Relative richness of bird edge species			
+ 6.31 SD^{rel}	0.10	0.14	4.94*
- 0.64 MPSD3^{rel}	0.04		
Relative abundance of white-footed mice			
+ 2.52 SD^{rel}	0.04	0.04	3.56*

[a] Abbreviations for landscape variables as in Table 1. For these analyses, relative change in variable calculated as $X^{rel}=X_{1996}/X_{1994}$.

Figure captions

Fig. 1. Location of study region on Little Mountain in George Washington National Forest, Virginia, USA.

Fig. 2. Landcover map of study area on Little Mountain displaying location of zone 1 (logged areas shown in white), zone 2 (area between cuts and red line), and zone 3 (all areas outside the red line). Black line shows boundary of lands managed by U.S. Forest Service.

Fig. 3. Map showing the area used to compute indices to characterize landscape structure at a survey point.

Fig. 4. Mean (±SE) bird richness for all species, interior species, and edge species. Richness values shown for different zones within the two years.

Fig. 5. Mean (±SE) presence for selected birds grouped by zones and year.

Fig. 6. Mean (±SE) abundance of white-footed mouse grouped by zones and year (zone, $\underline{F}=1.99$, $\underline{P}>0.05$; year, $\underline{F}=0.05$, $\underline{P}>0.05$; year×zone, $\underline{F}=6.49$, $\underline{P}<0.01$).

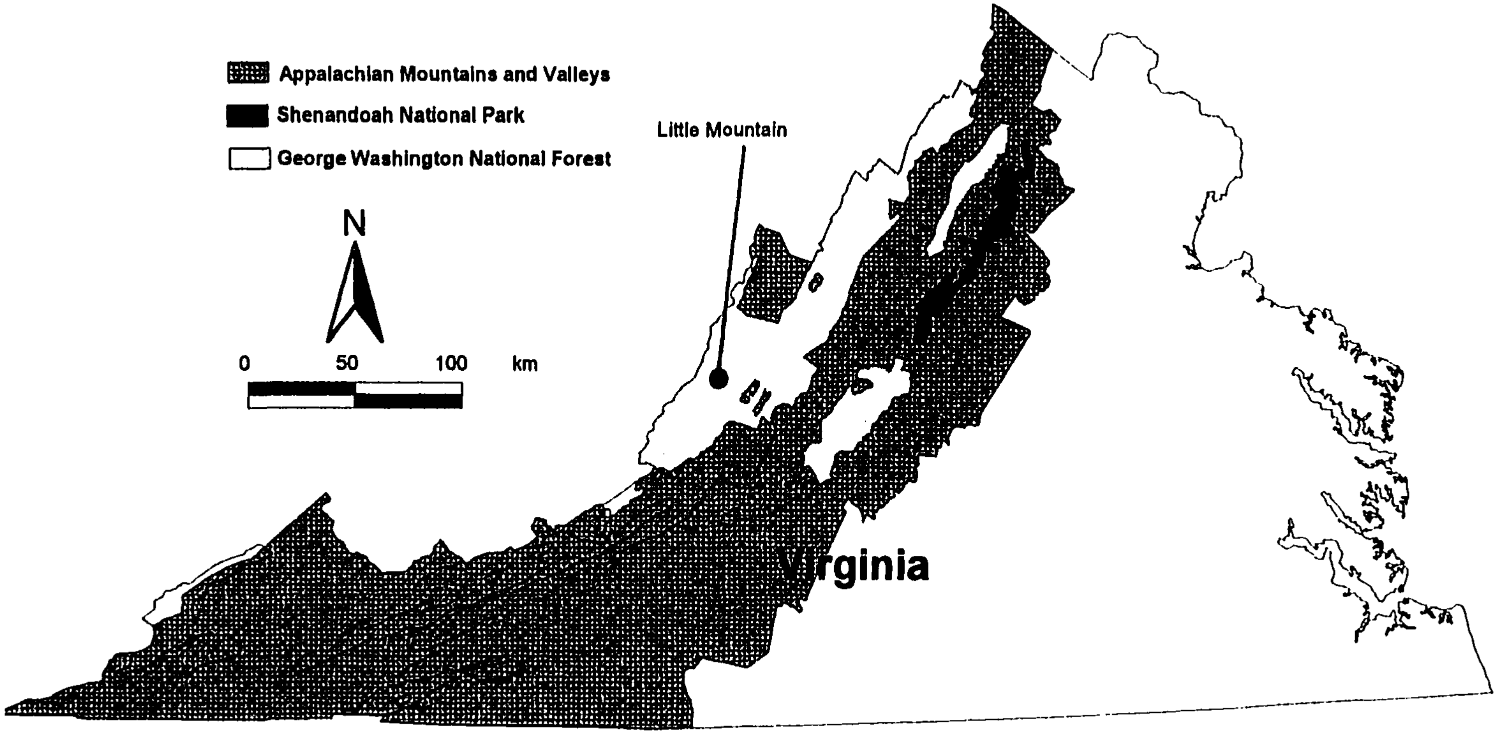

▨ Appalachian Mountains and Valleys
■ Shenandoah National Park
☐ George Washington National Forest
N
0
50
100
km
Little Mountain
Virginia

Fig. 1

Fig. 2


Logged areas
Early-successional deciduous forest
Midsuccessional deciduous forest
Mature deciduous forest
Early-successional mixed forest
Midsuccessional mixed forest
Early-successional coniferous forest
Midsuccessional coniferous forest
Water
Barren/Rock
Pasture
Field
Developed areas
Survey points
Landscape zones
Management unit
0
1
2
3
4 km
N

Fig. 3

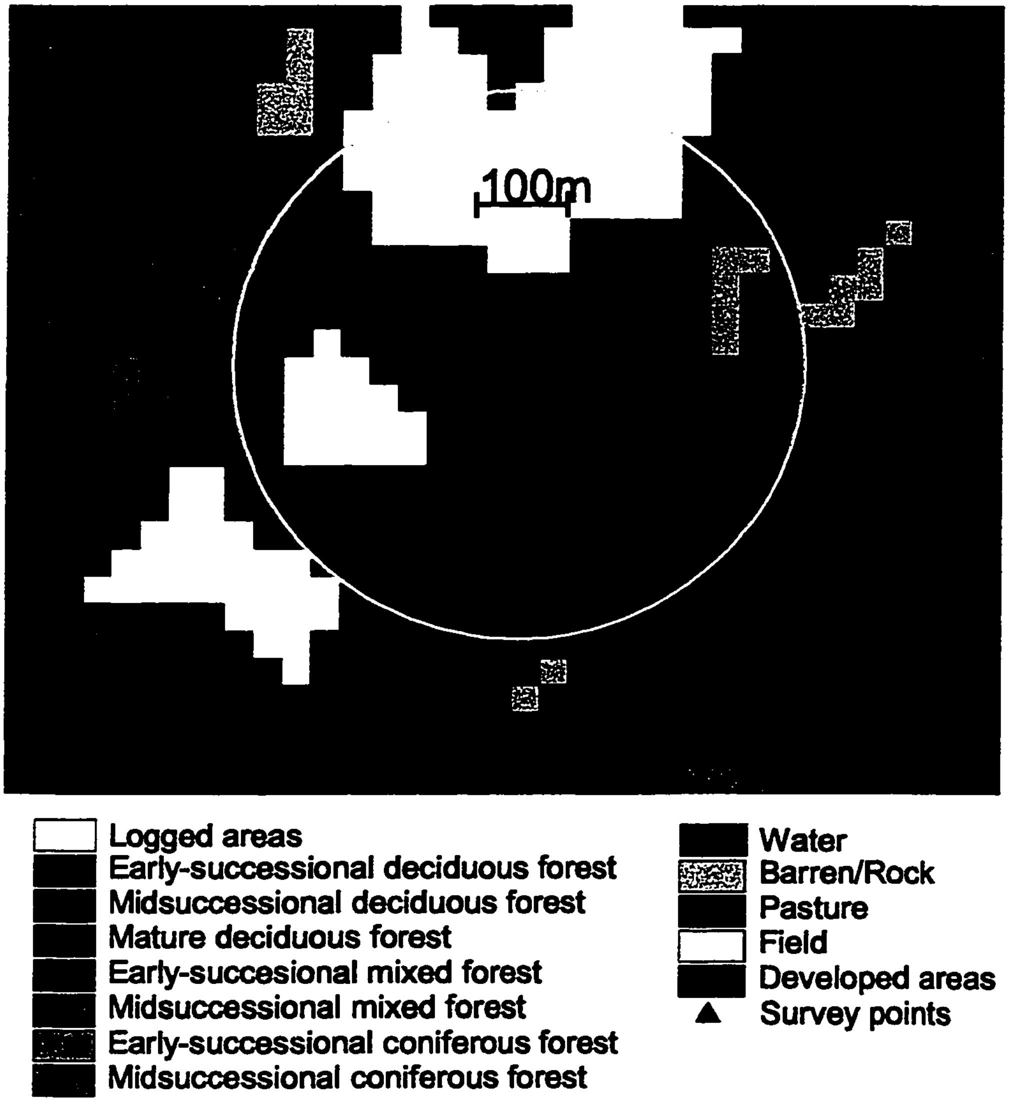

100m
Logged areas
Early-successional deciduous forest
Midsuccessional deciduous forest
Mature deciduous forest
Early-succesional mixed forest
Midsuccessional mixed forest
Early-successional coniferous forest
Midsuccessional coniferous forest
Water
Barren/Rock
Pasture
Field
Developed areas
Survey points

Fig. 4

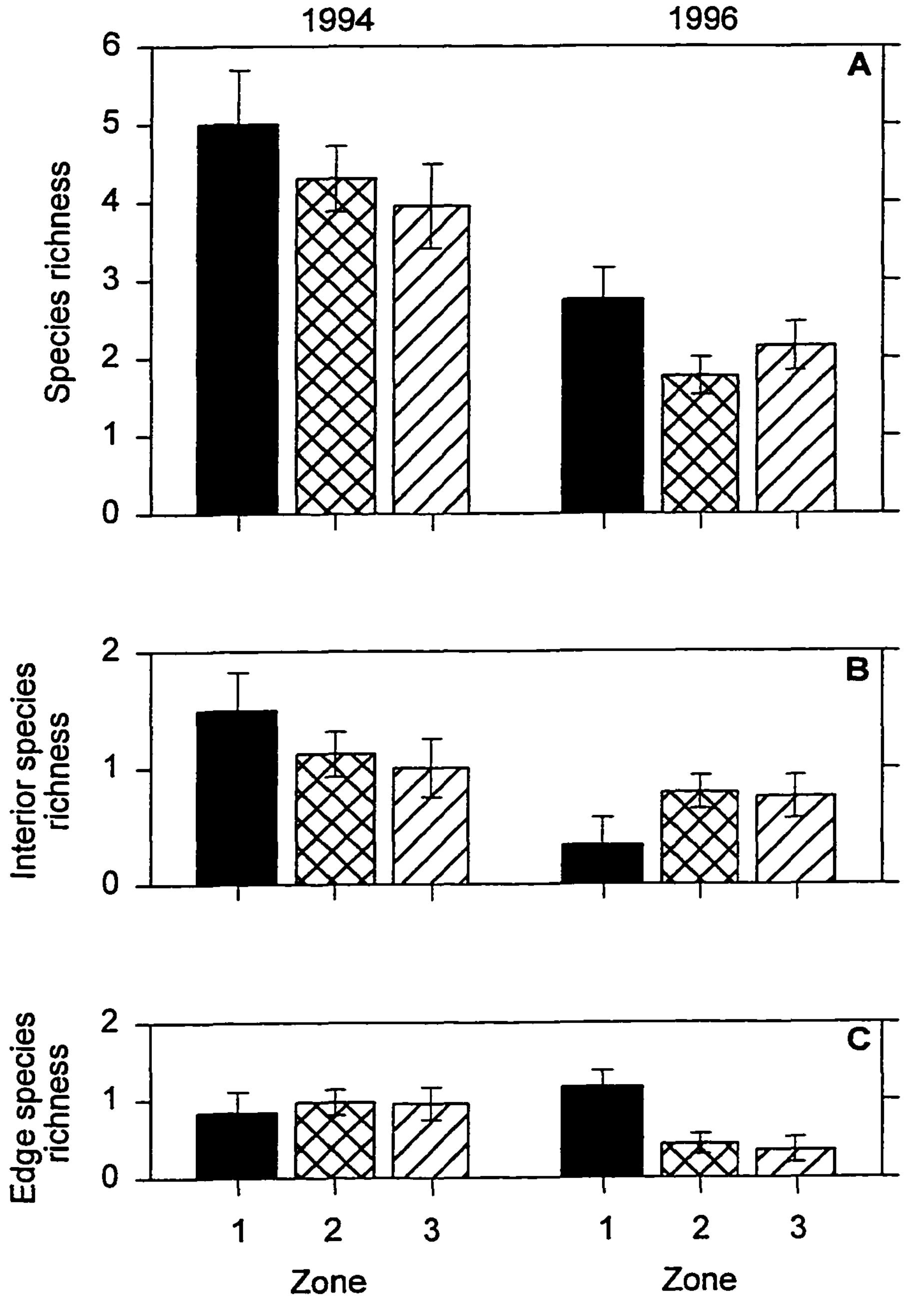

1994
1996
A
Species richness
0
1
2
3
4
5
6
B
Interior species richness
0
1
2
C
Edge species richness
0
1
2
1
2
3
Zone
1
2
3
Zone

Fig. 5

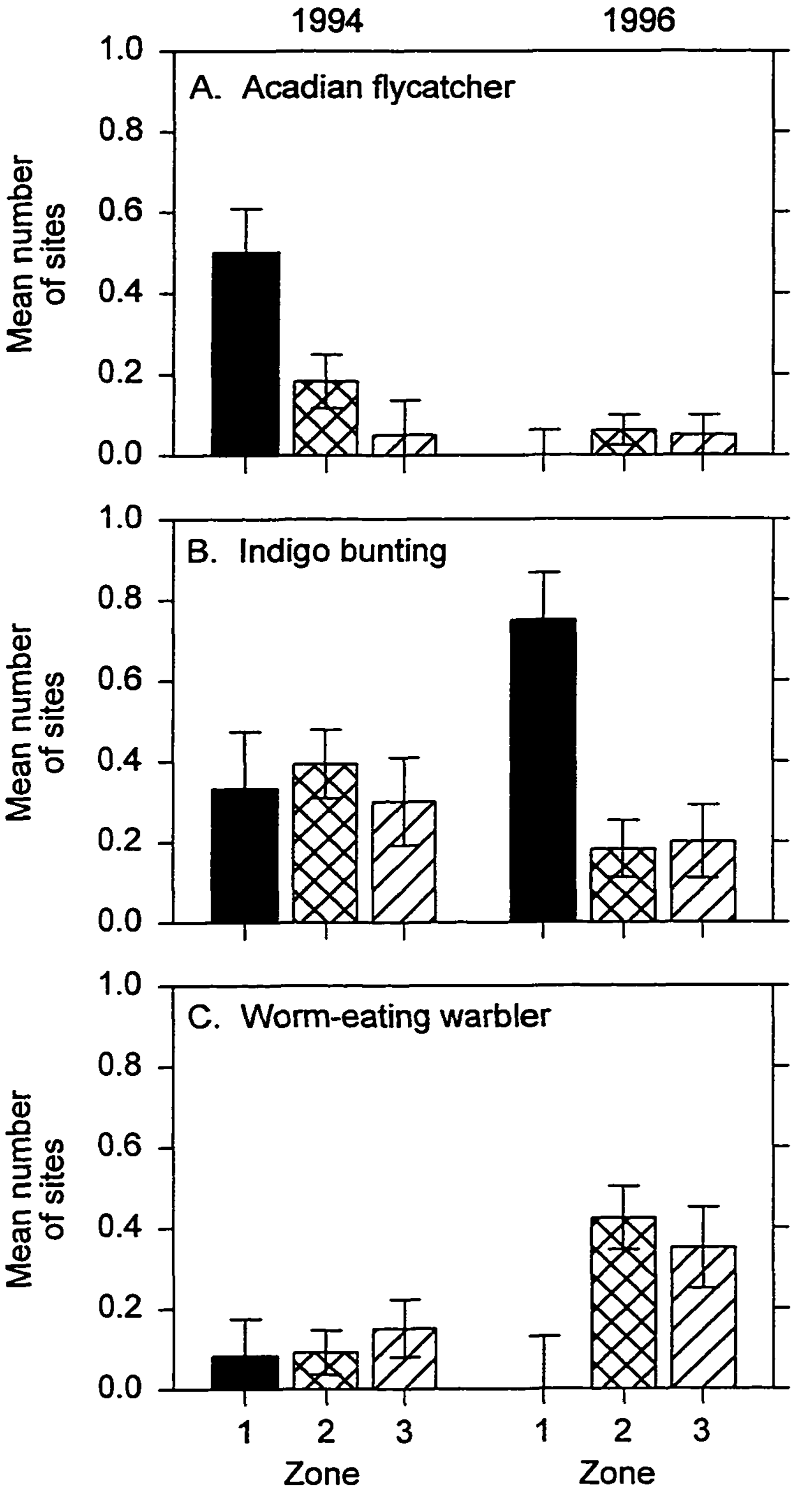

1994
1996
A. Acadian flycatcher
B. Indigo bunting
C. Worm-eating warbler
Mean number of sites
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
Zone

Fig. 6

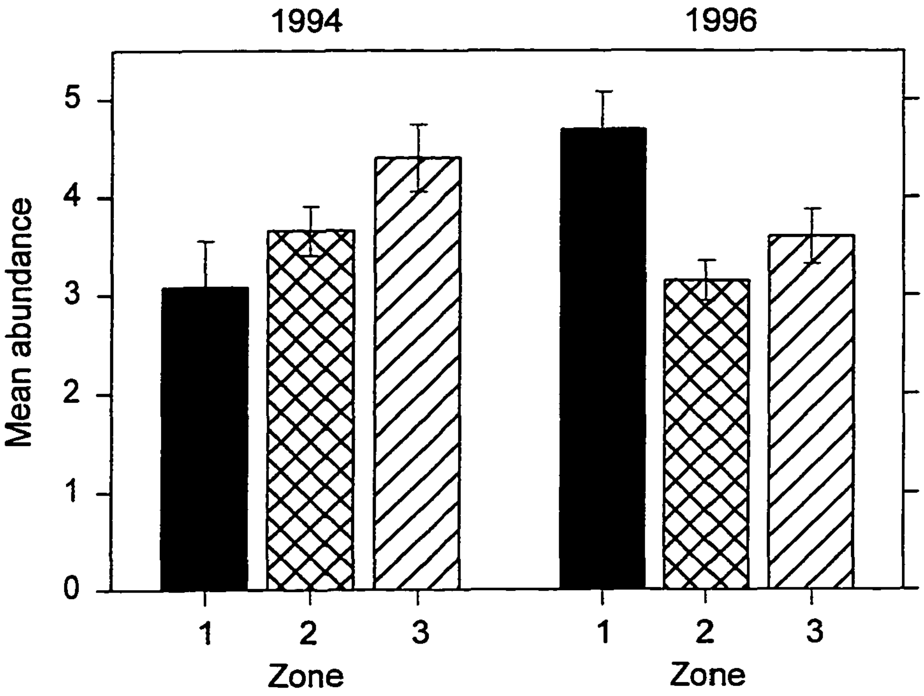
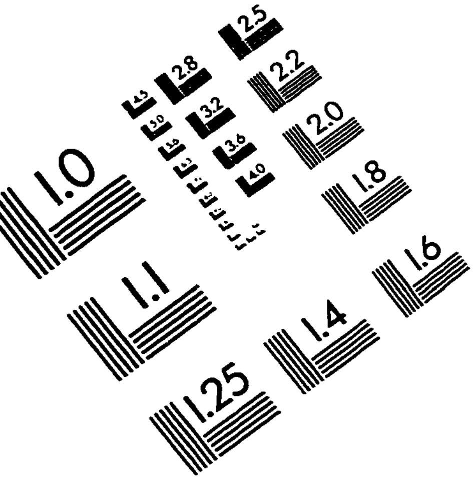
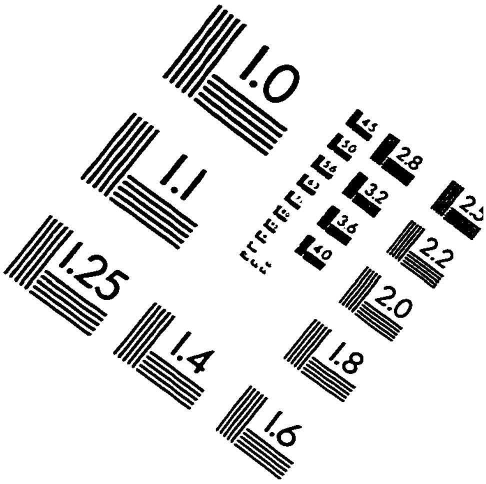
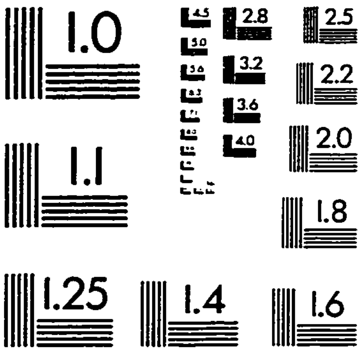
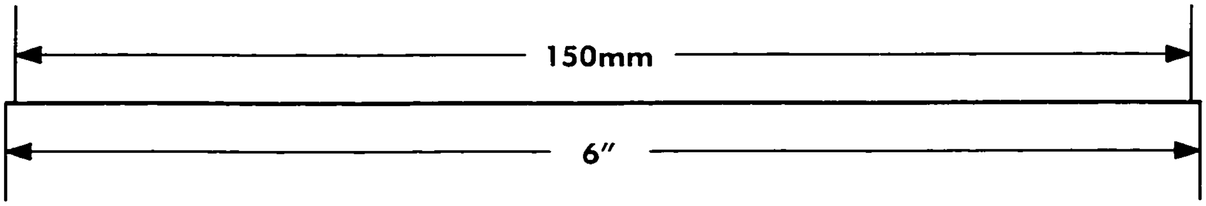


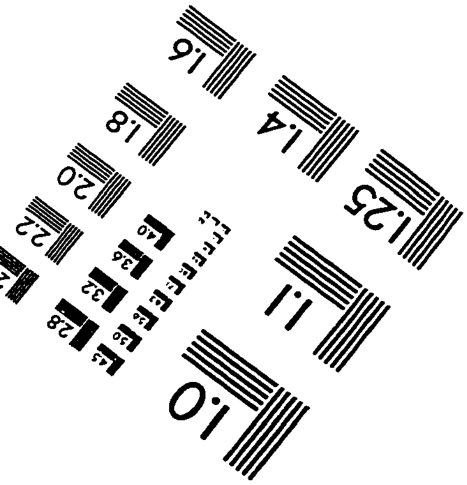
IMAGE EVALUATION TEST TARGET (QA-3)











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