

COMPARING SPATIAL PATTERN IN UNALTERED OLD-GROWTH AND DISTURBED FOREST LANDSCAPES¹

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Abstract. We used geographic information systems (GIS) to analyze the structure of a second-growth forest landscape (9600 ha) that contains scattered old-growth patches. We compared this landscape to a nearby, unaltered old-growth landscape on comparable landforms and soils to assess the effects of human activity on forest spatial pattern. Our objective is to determine if characteristic landscape structural patterns distinguish the primary old-growth forest landscape from the disturbed landscape. Characteristic patterns of old-growth landscape structure would be useful in enhancing and restoring old-growth ecosystem functioning in managed landscapes. Our natural old-growth landscape is still dominated by the original forest cover of eastern hemlock (*Tsuga canadensis*), sugar maple (*Acer saccharum*), and yellow birch (*Betula allegheniensis*). The disturbed landscape has only scattered, remnant patches of old-growth ecosystems among a greater number of early successional hardwood and conifer forest types.

Human disturbances can either increase or decrease landscape heterogeneity depending on the parameter and spatial scale examined. In this study, we found that a number of important structural features of the intact old-growth landscape do not occur in the disturbed landscape. The disturbed landscape has significantly more small forest patches and fewer large, matrix patches than the intact landscape. Forest patches in the fragmented landscape are significantly simpler in shape (lower fractal dimension, D) than in the intact old-growth landscape. Change in fractal dimension with patch size, a relationship that may be characteristic of differing processes of patch formation at different scales, is present within the intact landscape but has been obscured by human activity in the disturbed landscape. Important ecosystem juxtapositions of the old-growth landscape, such as hemlock with lowland conifers, have been lost in the disturbed landscape. In addition, significant landscape heterogeneity in this glaciated region is produced by landforms alone, without natural or human disturbances.

The features that distinguish disturbed and old-growth forest landscape structure that we have described need to be examined elsewhere to determine if such features are characteristic of other landscapes and regions. Such forest landscape structural differences that exist more broadly could form the basis of landscape principles to be applied both to the restoration of old-growth forest landscapes and the modification of general forest management for enhancing biodiversity. These principles may be particularly useful for constructing integrated landscapes managed for both commodity production and biodiversity protection.

Key words: biological diversity; disturbance; geographic information systems (GIS); hemlock-hardwoods; integrated management; landscape ecology; landscape structure; Michigan; old growth; reserve design; restoration; spatial statistics; Wisconsin; western Great Lakes.

INTRODUCTION

The concepts and principles of landscape ecology (Burgess and Sharpe 1981, Forman and Godron 1986) provide a framework for the quantitative analysis of landscape structure (Bowen and Burgess 1981, Romme 1982, Gardner et al. 1987, O'Neill et al. 1988, Johnson 1990, Turner and Gardner 1991). Applying these principles to interpret disturbance and other ecological pro-

cesses on the landscape (Turner 1987, Urban et al. 1987, Turner et al. 1989) can also provide a useful context for the design and management of landscapes for conserving biological diversity (Noss 1987, 1983), as well as for understanding the impacts of forest harvesting on landscape-scale ecological processes (Franklin and Forman 1987).

We are conducting a study designed to develop techniques for integrated landscape-scale forest management for a diverse forested landscape in northern Wisconsin, USA. The landscape contains scattered

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old-growth forest patches among a variety of early successional upland forest types. Remaining old-growth forest ecosystems have a variety of values for conservation of biological diversity, such as diverse structural habitat for vertebrates and invertebrates, mature forest interior habitat for birds, and genetic reserves and colonization sources for plant and animal species (Franklin et al. 1981, Crow 1990). Our goal is to take a broader landscape view of biodiversity management, beyond the narrow boundaries of the traditional, small old-growth forest preserve. We wish to place biodiversity management objectives, such as enhancing old-growth ecosystems, in a larger landscape context where the integrity and functioning of the old-growth ecosystem is buffered directly, but also enhanced by modified and integrated management of the larger harvested forest. Such an integration could be applied to a mixed-ownership landscape with contrasting gradients of management intensity and preservation, from core to outer area (e.g., Harris 1984, Noss and Harris 1986), or a national forest management unit with multiple management objectives. Ultimately, it is management of the larger forest matrix that must be modified to both protect natural diversity and maintain productivity (Franklin 1993, Mladenoff and Pastor 1993). However, very little old-growth remains in the Lake States, and any such remnants warrant consideration for enhancement.

As the first step in this process, we conducted a quantitative landscape analysis of the spatial pattern of a disturbed successional forest landscape containing scattered old-growth fragments, and compared this landscape to an intact old-growth landscape. This analysis was conducted to determine if there were discernible differences in landscape pattern and structure between a disturbed landscape and an old-growth landscape occurring on similar landforms. If such differences can be consistently described, information useful for evaluating ecological integrity of landscapes, and enhancing and restoring old-growth landscape structure can be derived. This information can also form part of the basis for further research that tests hypotheses relating to the functional importance of the observed patterns, information that will also be useful in enhancing biodiversity values of landscapes, while allowing forest harvesting where compatible with integrated landscape goals.

By the criteria of Hurlbert (1984) a comparison of two landscapes is pseudoreplicated, and statistical inferences cannot be derived that apply to the general classes of disturbed and old-growth landscapes. However, there are other considerations that make such comparisons valuable, and even necessary, if the caveat above is clearly stated. In a practical sense, we have carefully assessed the comparability of the two landscapes in terms of landform, soils, and original vegetation cover (see *Study region*). In addition, *Sylvania* is the only remaining old-growth hemlock-hard-

wood landscape of its size on a relatively uniform landform in the western Lake States, thus making replication impossible. However, even single landscapes, such as the subject of our study, contain hundreds of varying individual patches. Thus each landscape is a large collection of separately responding units, distinguishing these landscape comparisons in some degree from unreplicated studies containing simpler, single-treatment units. The difficulty and cost of high-resolution, large-scale landscape comparisons also often make replication prohibitive. We believe that unreplicated comparisons can provide useful insight and results to be tested and compared more broadly. These useful results must be produced with care in interpretation and attention to landscape characteristics that make a given comparison valid.

At any scale of observation, spatial heterogeneity results from the interaction of natural processes and human activities on the landscape. When viewed at a coarse-grained scale (such as 1:250 000 to 1:10⁶), human activities reduce spatial heterogeneity in mixed agricultural/forest landscapes (Krummel et al. 1987, O'Neill et al. 1988). This is particularly true where spatial heterogeneity is defined as land cover patch shape. However, at finer grained scales within an entirely forested landscape, other factors such as natural disturbance and community and ecosystem responses produce a more complex landscape pattern of forest types (Pastor and Broschart 1990).

The components of landscape pattern can be described in several ways: (1) patch type diversity (number of different patch types), (2) number of patches, (3) patch type distribution across the landscape, (4) association and dispersion relationships between types, and (5) patch complexity, or size and shape (Forman and Godron 1986). From these components various indices and models of landscape processes and change can be constructed, and related to their effect on ecosystem processes, forest community dynamics, or species habitat (Fahrig and Merriam 1985, Gardner et al. 1987, Turner 1987, O'Neill et al. 1988, Milne et al. 1989). Such information, not previously obtainable at the landscape scale without GIS, will be crucial in developing landscape-scale reserve design, and management objectives and prescriptions that have the greatest potential of restoring natural processes that depend upon a particular landscape structure.

STUDY REGION

Our study compares two forested landscapes of similar area, landform, and soils but different in land use history. The disturbed landscape, referred to as the Border Lakes and Forest Area, is a 9600 ha area in northern Wisconsin along the upper Michigan border, USA (46°12' N, 89°34' W). This is a forested, glacial landscape with numerous lakes and wetlands typical of the upper Great Lakes Region. Successional hardwood and conifer forest types dominate, but the area

also contains fragmented patches of remnant old-growth northern hardwood and hemlock forest.

The intact landscape is the Sylvania Wilderness in the Ottawa National Forest, Michigan, ≈ 10 km east of the disturbed landscape. Sylvania is a landscape of primary forest, nearly all of which is old-growth hemlock-hardwoods. Both landscapes are located on the same end moraine landform (Attig 1985) and are dominated by the same major soil types (Jordan 1973, Natzke and Hvizdak 1988, J. K. Jordan, *personal communication*). An examination of witness tree data recorded by the original land surveyors revealed that the Border Lakes landscape was originally dominated by eastern hemlock (*Tsuga canadensis*), as Sylvania remains today (Laska et al. 1981, Spies and Barnes 1985). Both of these study areas are within the boreal-northern hardwood forest transition region (Pastor and Mladenoff 1992). Because of this transition region, the disturbed Border Lakes landscape has a diverse assemblage of successional forest ecosystems. The young stands of the Border Lakes landscape contain tree species characteristic of both the boreal and northern hardwood regions, with combinations varying with site characteristics and history.

Climate in this region is characterized by summers that are short and mild, and long and cold winters with snow cover from November to April. Annual precipitation is ≈ 85 cm, and mean temperatures are $\approx -10^\circ\text{C}$ for January and 18°C for July.

METHODS

Data sources

An analysis of the relation of the Sylvania forest landscape to soils and topography was done by Pastor and Broschart (1990). We followed similar methods of data acquisition and processing for the Border Lakes landscape to facilitate comparison with Sylvania. We mapped vegetation patch types of the study landscape based on interpretation of 1:24 000 color infrared stereo photography taken on 1 May 1980 (leaf-off for deciduous species). The minimum mapping unit was < 1.0 ha for forest types, and < 0.5 ha for discrete wetland patches and patches defined by roads. The map was updated by comparing it to low-altitude color infrared photography (1:6000 scale imagery) flown at peak fall color in September 1989. Forest type signature was field verified twice during summer 1989. The forest map was transferred to a mylar overlay on 1:24 000 USGS topographic maps using a Bausch and Lomb zoom transfer scope. The overlay was digitized using the ARC/INFO geographic information system (ESRI 1987) on an MS-DOS compatible microcomputer.

Map creation

Maps were analyzed using ARC/INFO software on both microcomputer and VAX mainframe computers. Landscape structure of the Border Lakes area was compared with the less disturbed Sylvania landscape by

entering the map data of Pastor and Broschart (1990) into ARC/INFO, and selectively re-analyzing their data and the Border Lakes using the same techniques.

To examine landscape structure due to natural disturbance upon the basic geomorphology, we used the detailed patch type map of the Sylvania landscape, assuming that this largely undisturbed landscape approximates the original condition of the Border Lakes landscape. Conversely, the detailed patch type map of the Border Lakes Area reflects the sum of all sources of heterogeneity, resulting from 100 yr of human activity imposed upon conditions that predated European settlement.

Analysis

Using these maps, we summarized patch type, area, number, size class distribution, and importance on the two landscapes. Several additional analyses were done to further describe landscape complexity. Differences in the patch size class distributions between Sylvania and Border Lakes ecosystem types were tested using the nonparametric Kolmogorov-Smirnov test (Sokal and Rohlf 1981). We also calculated two indices based on the Shannon-Wiener information theory index (Shannon and Weaver 1962), which describe overall landscape structure (Turner and Ruscher 1988). Landscape diversity is calculated by:

$$H = - \sum_{k=1}^m (P_k) \log(P_k),$$

where P_k is the proportion of the landscape in ecosystem type k , and m is the total number of types on the landscape. The value of H increases with greater landscape diversity. Landscape dominance is calculated by:

$$d = H_{\max} + \sum_{i=1}^m (P_i) \log(P_i),$$

where m is the total number of types on the landscape and P_k is the proportion of the landscape in ecosystem type k . This index conveys dominance by indicating the deviation from the maximum possible value; H_{\max} has the effect of normalizing the index between landscapes of unequal numbers of patch types (Turner and Ruscher 1988).

Fractal analysis was used to quantify the complexity of patch size and shape relationships (Mandelbrot 1977). We used an area/perimeter relation to calculate the fractal dimension of patches by ecosystem type (Krummel et al. 1987, Sugihara and May 1990), using the method of successive linear regression of $\log(\text{Area})$ against $\log(\text{Perimeter})$ (Krummel et al. 1987, Pastor and Broschart 1990) where the fractal dimension (D) equals twice the slope of the regression line. Confidence limits (95%, as in Fig. 3) were similarly calculated as twice the confidence limit of the slope. Values of D near 1.0 indicate simple shapes approaching those of a circle, while values near 2.0 describe shapes with

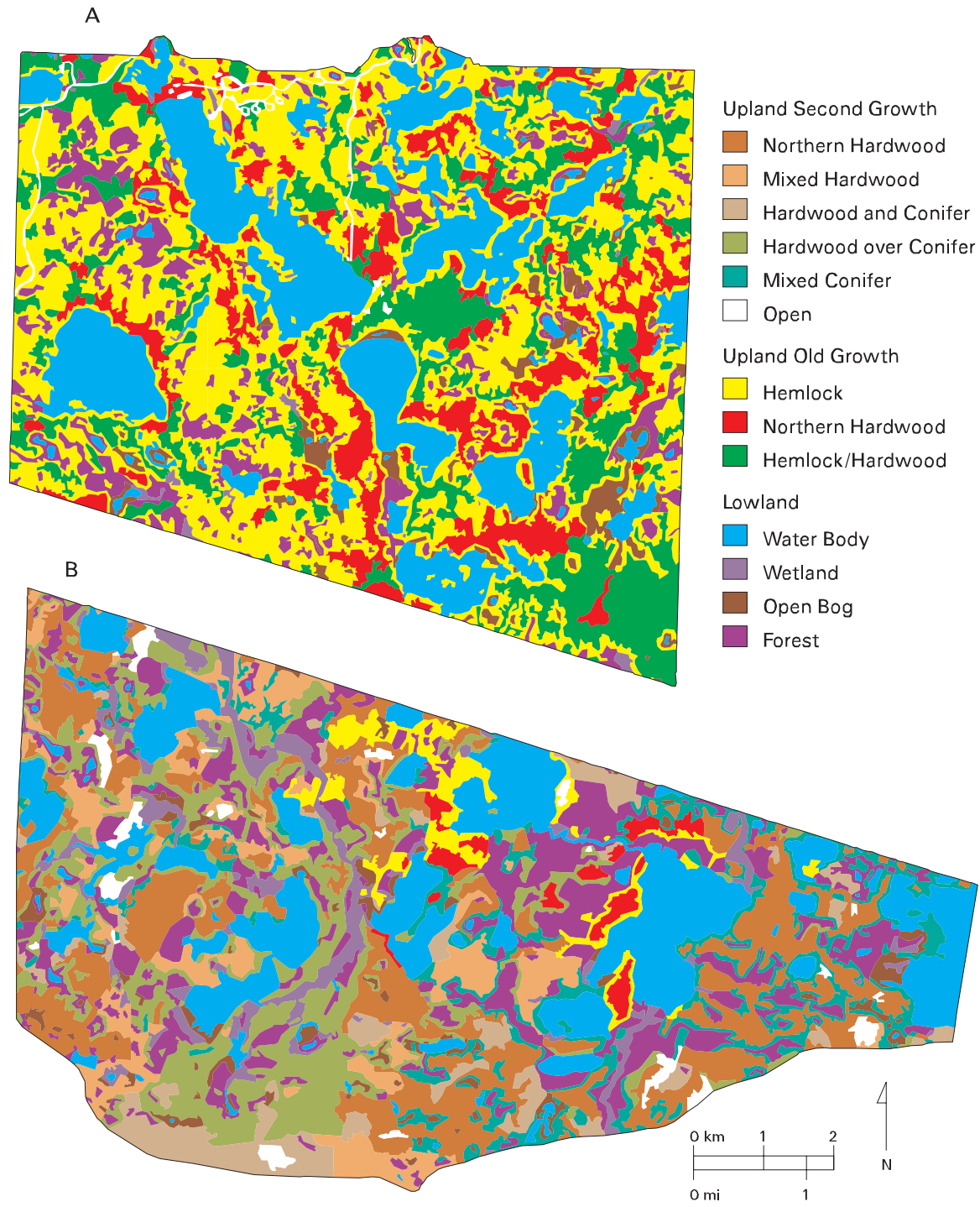


FIG 1. (A) Sylvania Wilderness landscape patch types. (B) Border Lakes landscape patch types.

maximum complexity. The method of Krummel et al. (1987) was modified by calculating regressions on those points within a 0.6-m² sliding window along the *x* axis, incrementing by 0.2 m², rather than a sliding window of a fixed number of points, to give finer spatial res-

olution to the resulting graphs. Additional criteria for the individual regressions were a 20-point minimum and *P* < .05. Confidence limits were calculated for each value of *D* to assess the significance of differences observed across patch sizes. We compared values of *D*

TABLE 1. Patch type summary for Border Lakes and Sylvania landscapes in the western Great Lakes region of the USA.

	Area (ha)		Percent area		Patch number		Percent patches		
	Border	Sylvania	Border	Sylvania	Border	Sylvania	Border	Sylvania	
			Old growth						
Lakes	1624.16	1531.15	16.80	21.26	105	71	6.14	9.69	
Wetland	423.39	43.52	4.38	0.60	140	43	8.18	5.87	
Bog	212.89	211.13	2.20	2.93	100	107	5.84	14.60	
Lowland conifer	1362.21	601.18	14.09	8.35	350	206	20.46	28.10	
Hemlock	222.97	2673.92	2.31	37.12	19	113	1.11	15.42	
Northern hardwood	114.60	846.21	1.19	11.75	19	84	1.11	11.46	
Hemlock/hardwood	...	1234.04	...	17.13	...	95	...	12.96	
			Second growth						
Northern hardwood	1843.82	...	19.07	...	238	...	13.91	...	
Mixed hardwood	1333.14	...	13.79	...	154	...	9.00	...	
Hardwood/conifer	406.06	...	4.20	...	56	...	3.64	...	
Hardwood over conifer	1370.50	...	14.17	...	261	...	16.98	...	
Mixed conifer	615.54	...	6.36	...	206	...	12.04	...	
Upland openings	139.78	61.63	1.45	0.86	37	14	2.16	1.91	
			Total						
	9669.06	7202.79			1711	733			

between Border Lakes and Sylvania using the regression line slope comparison procedure of Sokal and Rohlf (1981).

We evaluated adjacency or contagion between different ecosystem patches by calculating the electivity index of Jacobs (1974) and Jenkins (1979) as used by Pastor and Broschart (1990):

$$E_{ij} = \ln[(r_{ij})(1 - p_{ij}) / (p_{ij})(1 - r_{ij})],$$

where E_{ij} is the electivity index for nearest neighbor probabilities calculated for patch types i and j , with r_{ij} the proportion of shared perimeter of type i around type j , and p_{ij} the proportion of shared perimeter of type i around all other patch types except type j . Values generated by the electivity index are compared with the chi-square distribution for significance levels.

This index provides a measure of positive or negative association, or independence between a given patch type and other ecosystems. The data were generated using the ARC/INFO system to map a 20-m band around each ecosystem type patch, which reveals the category and relative perimeter amount of the adjacent patches (Pastor and Broschart 1990).

RESULTS

Patch distribution and landscape diversity

The Sylvania map reveals a natural landscape structure resulting from combined landform and natural disturbance factors (Fig. 1A, Table 1). In the Sylvania Wilderness, the upland areas consist entirely of old-growth mesic forest of: (1) eastern hemlock (*Tsuga canadensis*) dominated stands, (2) hardwood-dominated stands, primarily composed of sugar maple (*Acer saccharum*), with yellow birch (*Betula allegheniensis*) and basswood (*Tilia americana*), and (3) stands containing a mixture of hemlock and hardwoods (Pastor and Broschart 1990).

In the Border Lakes Area there are seven upland

forest types including two old-growth forest ecosystems (Fig. 1B, Table 1). Old-growth forests constitute <3.5% of the total Border Lakes landscape, or 5.7% of the total upland forest. The most abundant forest types as a percent of the total landscape are second-growth northern hardwoods (19.1%), now primarily sugar maple; a mixture of birch-aspen hardwoods (*Betula papyrifera*-*Populus tremuloides*) over understory conifers, primarily balsam fir (*Abies balsamea*) (14.2%); and a mixed hardwoods (birch-aspen) type (13.8%) without the conifer understory. Less important is an upland mixed conifer type, with patches composed of white spruce (*Picea glauca*), fir, white pine (*Pinus strobus*), hemlock, and white cedar (*Thuja occidentalis*) (6.4%).

Like the Sylvania Area, most old-growth patches on the Border Lakes Area are small, nearly all <10 ha, although there are many fewer patches ($n = 38$) than in Sylvania ($n = 292$) (Fig. 1B, Table 1). The mean size of upland forest patches (old-growth) in Sylvania is ≈ 16.4 ha (median 4.22 ha, range 0.10–1019.0 ha). The mean patch size of dominant upland second-growth forest on Border Lakes is 6.7 ha (median 2.48 ha, range 0.10–163.89 ha), with the remnant old-growth mean size 8.88 ha (median 6.14 ha, range 0.38–67.72 ha) (Table 1). However, among the several second-growth types, patch sizes are more variable; the hardwood types vary with means of 9.60 and 10.93 ha (medians 2.90 and 4.70 ha, range 0.20–163.40 ha), while the mixed-conifer type mean size is 3.40 ha (median 1.63 ha, range 0.27–48.57 ha) (Table 1).

As suggested by the high standard deviations in Table 1, patch size distribution is very skewed within each ecosystem type (Fig. 2). For Sylvania, hemlock is the dominant ecosystem type, with large patches forming the landscape matrix (Pastor and Broschart 1990). The very abundant small patches are dispersed across the landscape (Figs. 1A and 2A). More importantly, the

TABLE 1. Continued.

Patch size mean \pm 1 SD		Patch size median	
Border	Sylvania	Border	Sylvania
Old growth			
15.47 \pm 47.69	21.57 \pm 58.27	2.44	2.10
3.02 \pm 6.48	1.98 \pm 16.30	1.16	4.00
2.13 \pm 2.32	1.01 \pm 31.60	1.30	5.60
3.89 \pm 8.23	2.92 \pm 5.94	1.60	1.37
11.74 \pm 16.03	21.57 \pm 101.06	9.12	3.10
6.03 \pm 5.18	10.08 \pm 16.30	5.15	4.00
...	12.99 \pm 31.60	...	5.60
Second growth			
7.75 \pm 18.54	...	2.09	...
8.66 \pm 18.16	...	2.82	...
7.25 \pm 14.99	...	3.24	...
5.25 \pm 10.03	...	2.10	...
2.99 \pm 5.39	...	1.40	...
3.78 \pm 4.20	4.40 \pm 9.97	1.91	0.59
Total			
5.65 \pm 16.92	9.83 \pm 46.17	1.81	1.85

percent area graph (Fig. 2B) shows that larger patches >40 ha (>1000 ha for hemlock) dominate >80% of the landscape, although comprising only \approx 9% of the hemlock patches.

For the Border Lakes, no single matrix patch type dominates, and the patch number to area relations are also less clear (Fig. 2C–H). There are greater proportions of patches in the smallest size class, and less dominance of the larger sizes in total area. The mixed-conifer type, which appears to occupy sites similar to hemlock in Sylvania (Fig. 1), suggests the most fragmented patch structure (Fig. 2C, D). In the most abundant northern hardwoods type there is only 45% of the total patch area in the largest size class (Fig. 2E, F). Additionally, these patches range to only 150 ha in size, compared to >1000 ha for the dominant hemlock in Sylvania (Table 1). The remaining old growth in Border Lakes also shows a loss of these large, dominant patches, although less severely than the second-growth types. Size class distributions of the major second-growth types shown (Fig. 2) are significantly different from that of the dominant old-growth hemlock ecosystem of Sylvania, as is a collective comparison between Border Lakes and Sylvania of all upland forest patches (Kolmogorov-Smirnov test, all $P < .005$).

Because the dominant hemlock matrix has been replaced with a variety of second-growth forest types, landscape diversity is higher on Border Lakes than Sylvania ($H = 2.17$ vs. 1.63), but dominance is higher on Sylvania ($d = 0.45$ vs. 0.31) than Border Lakes.

Adjacency analysis

Spatial associations among the forest types of the two landscapes reveal changed relationships caused by anthropogenic disturbance, producing greater fragmentation and proliferation of successional types on Border Lakes. The patch type associations of Border Lakes are considerably more complex due to the greater

number of patch types present on the site than on the less disturbed Sylvania landscape (Table 2). The strong positive association between hemlock and lowland conifers on Sylvania has been lost on the disturbed Border Lakes landscape, where old-growth hemlock is now distributed independently of lowland conifers. Pastor and Broschart (1990) and Spies and Barnes (1985) suggest that these lowlands provide a refuge for hemlock during climatically dry periods, and provide a seed source for establishment on adjacent uplands when conditions are appropriate. If this is so, then the adjacency analysis suggests that patch types that are now positively associated with lowland conifers likely occupy former hemlock sites. Since these sites are the mixed conifer, and hardwood and conifer types, this may be a plausible explanation suggesting that the former hemlock sites still favor conifers. Conversely, purely hardwood types tend to have negative associations or none with lowland conifers (Table 2). The significant associations in Table 2 are not symmetrical about the diagonal because of the nature of the landscape relations between several patch types, which do not exhibit reciprocal associations. An extreme example is a matrix type, in which all other types are embedded. Each embedded type will be highly associated with the matrix, but the matrix will be equally associated with all types.

Associations of the remnant Border Lakes old-growth types are largely an artifact of the human disturbance that occurred, primarily past logging patterns that largely bypassed them, although many of these patches received some selective cutting. Thus old-growth hemlock and hardwoods are positively associated only on Border Lakes, since all old-growth remnants occur in the same portion of the landscape. Old-growth hardwoods, which are negatively associated with lowland conifers on Sylvania, have lost this spatial relationship on Border Lakes, showing an independent distribution (Table 2).

Fractal analysis

In calculating measures based on patch shape or complexity of map data, it is possible for results to be biased due to patches contacting the artificial edges of the map (Gardner et al. 1987). We dealt with this problem in the following way. On the Border Lakes landscape, most map edges reflect real landscape boundaries, such as lakes (east edge) or roads (south edge) that define actual patch boundaries. To test for possible bias due to artificial edges, we calculated D for the northern hardwood patch type, which has the greatest contact with map edges of all types on Border Lakes. For all northern hardwood patches $D = 1.30$, and for only interior patches $D = 1.35$. We tested for significance with the regression line comparison procedure of Sokal and Rohlf (1981) and found the difference not significant ($P > .05$).

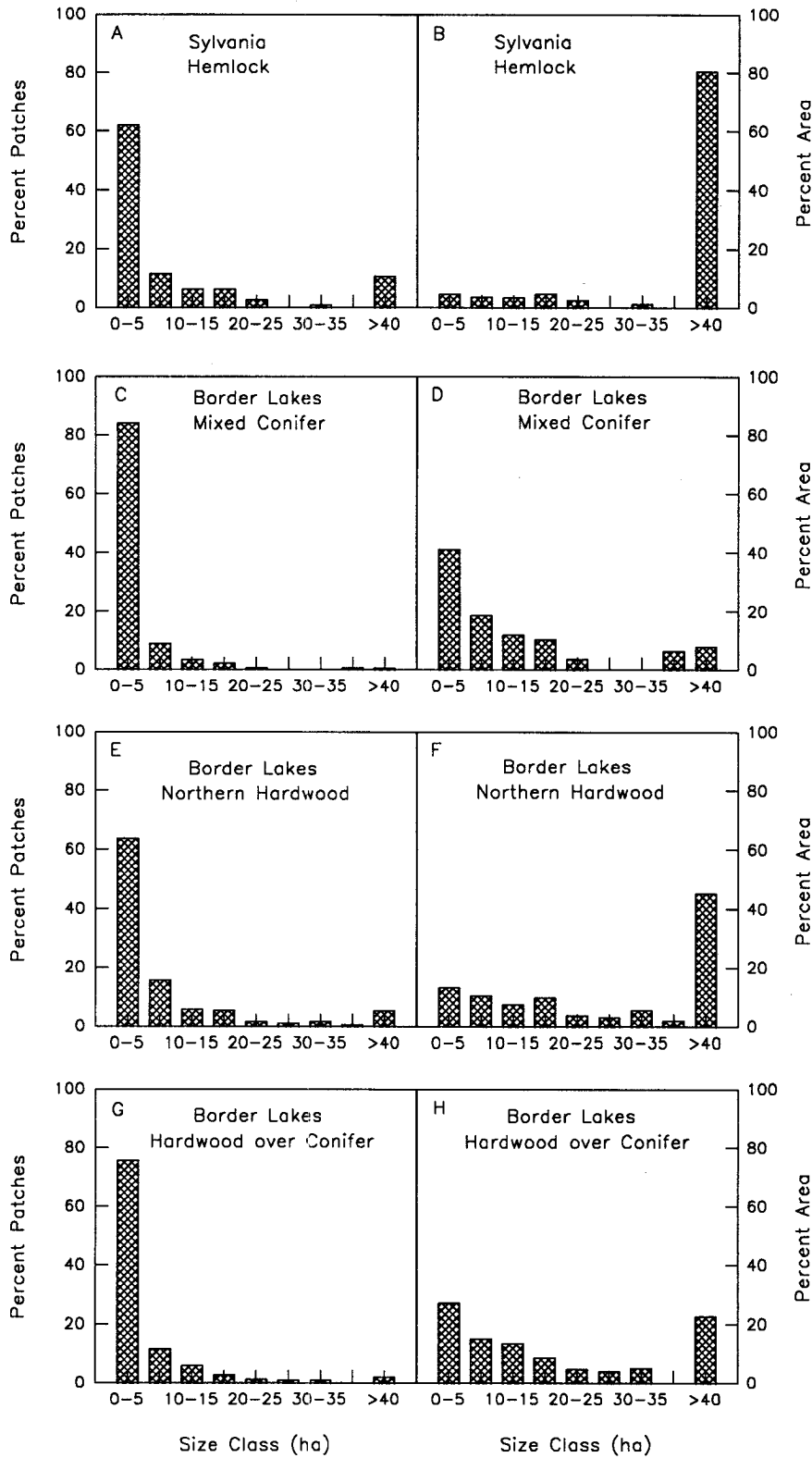


FIG. 2. Patch area and size class distributions for dominant Sylvania and Border Lakes forest types. Patch size class distributions of Border Lakes successional forest types (C, E, G) are significantly different from those of Sylvania old growth (Kolmogorov-Smirnov test, $P < .005$).

TABLE 2. Adjacency analysis of ecosystem types in Border Lakes (upper symbols) and Sylvania (lower symbols) landscapes. Symbols indicate positive (+) and negative (-) association or independence (0) or type not present (...). Association shown for $\chi^2 > 7.78$, 1 df, $P < .005$.

	Old growth				Second growth				
	LC	HE	NHD	H/HD	NHD	MHD	H/C	HOC	MC
					Old growth				
Lowland conifer (LC)		0 +	- -	... -	- ...	0 ...	0 ...	+ ...	0 ...
Hemlock (HE)	0 0		+ 0	... 0	0 ...	0 ...	0 ...	- ...	- ...
Northern hardwood (NHD)	0 -	+ +		... 0	0 ...	0 ...	0 ...	0 ...	0 ...
Hardwood/hemlock (H/HD)	... -	... +	... 0
					Second growth				
Northern hardwood (NHD)	- ...	0 ...	0		0 ...	+ ...	0 ...	+ ...
Mixed hardwood (MHD)	0 ...	0 ...	0	0 ...		0 ...	+ ...	0 ...
Hardwood/conifer (H/C)	0 ...	0 ...	0	+ ...	0 ...		0 ...	- ...
Hardwood over conifer (HOC)	+ ...	0 ...	-	0 ...	0 ...	0 ...		- ...
Mixed conifer (MC)	+ ...	- ...	0	+ ...	0 ...	0 ...	- ...	

On Sylvania, the most abundant patch type, which is also in greatest contact with map edges, is the old-growth hemlock. This type also forms the landscape matrix. We found that eliminating the hemlock edge polygons would remove most of this important type because of the large patch size and complexity. As a test we proceeded with the analysis with all hemlock polygons. As the results show, the Sylvania landscape and the hemlock type specifically have higher values of D than Border Lakes, and therefore the greatest patch complexity (Table 3). Even including map edges on Sylvania, our results are in fact conservative for the complexity of Sylvania patch types.

Fractal dimensions calculated for major upland forest ecosystems on the Border Lakes Area (Table 3) vary from $D = 1.08$ and 1.35 (old-growth types) to 1.45 for mixed conifers. Fractal dimensions for upland forest patches overall are significantly different between Border Lakes ($D = 1.29$) and Sylvania ($D = 1.44$; $P < .005$). On Sylvania, the upland old-growth forest types all have fractal dimensions of 1.40 – 1.47 , exceeding all Border Lakes forest types except mixed conifers. The similarity between Sylvania old-growth hemlock and Border Lakes mixed-conifer types is consistent with the areal (Fig. 1) and adjacency analyses, and suggests that the mixed-conifer patches occupy former hemlock sites.

Plotting D against $\log(\text{Area})$ reveals that the different ecosystems exhibit variation in D over a range of scales (Fig. 3). But in calculating D using 20-point patch size increments, the wide confidence limits indicate that only selected size classes have a fractal dimension that

deviates significantly from random ($D = 1.5$) when compared at this resolution. In general, patch types on the Border Lakes landscape have lower variability when compared to Sylvania. Border Lakes forest types of mixed conifers, hardwood over conifer, and northern hardwood all have patch size classes with D significantly lower than random (< 1.5) in the smaller sizes (Fig. 3). Northern hardwood patches are also significantly simpler than random in larger patch sizes, $\log(\text{Area}) 4.6$ – 5.4 . Although the mixed-conifer type has the highest fractal dimension of all the Border Lakes forest types, this type has the smallest range of patch sizes of any type (0.27–48.57 ha).

TABLE 3. Fractal dimension (D) calculated for Border Lakes and Sylvania upland forest ecosystems ($r^2 > 0.87$, $P < .001$).

	D	N
Border lakes		
Old growth		
Hemlock	1.35	20
Hemlock/hardwood	1.24	18
Second growth		
Northern hardwood	1.29	192
Mixed hardwood	1.30	122
Hardwood/conifer	1.08	56
Hardwood over conifer	1.33	261
Mixed conifer	1.45	181
All upland forest	1.29	850
Sylvania		
Old growth		
Hemlock	1.45	113
Northern hardwood	1.47	95
Hemlock/hardwood	1.40	84
All upland forest	1.44	292

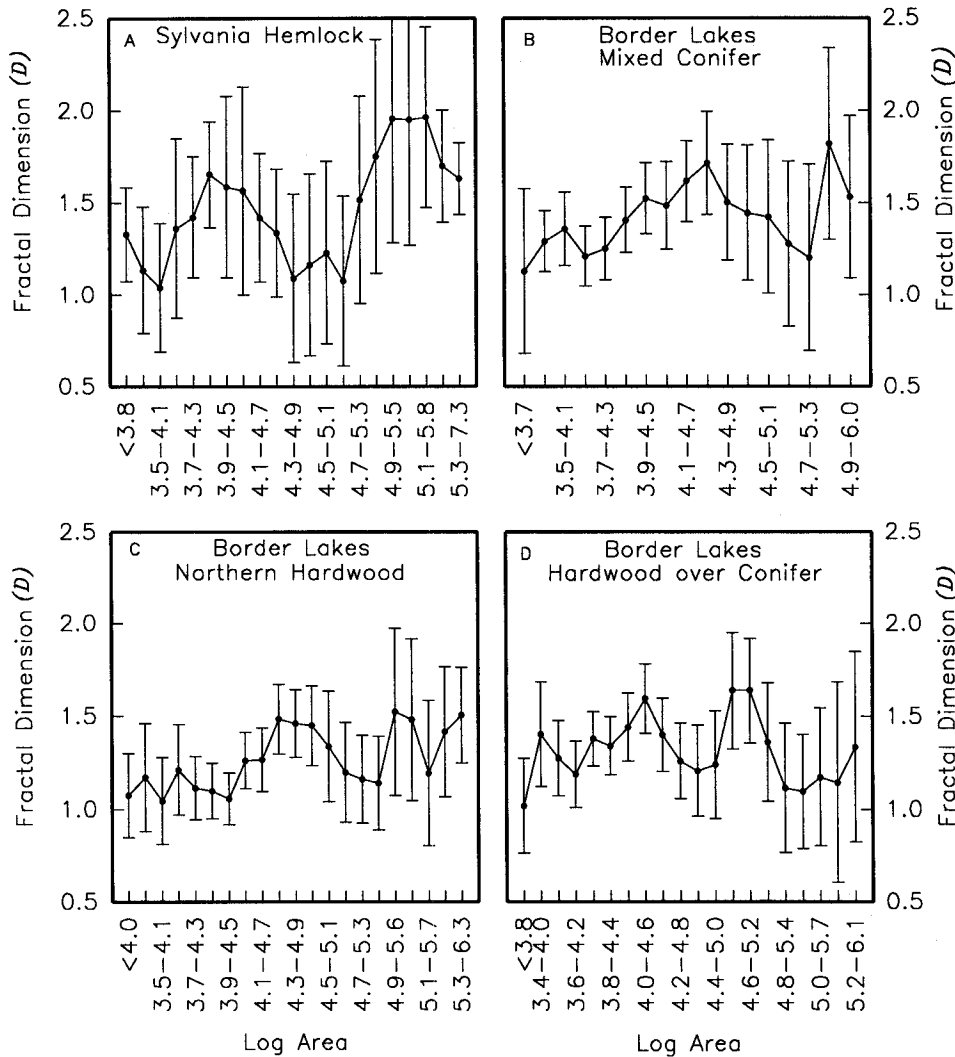


FIG. 3. Plots of fractal dimension (D) vs. area (measured in square metres) for dominant Border Lakes and Sylvania landscape forest types. Vertical bars are 95% confidence limits. Overall fractal dimensions of Border Lakes ecosystem types (B, C, D) are significantly different from those of Sylvania (A; $P < .005$). Within a single type, only Sylvania hemlock (A) contained different patch size areas of significantly different fractal dimension ($P < .05$; $\log(\text{Area}) < 4.6$ vs. $\log(\text{Area})$ 5.2–7.3).

In Sylvania, upland forest types have values of D that often approach 2.0, particularly in middle and larger patch sizes. Variability, as shown by the wider confidence limits, is generally greater within patch types on Sylvania than Border Lakes. This higher variability for Sylvania and lower variability for Border Lakes is consistent with the greater patch complexity on Sylvania. Distinctive peaks and valleys are generally fewer and more extreme on Sylvania than on Border Lakes. Additionally, values of D for Sylvania are likely to be conservative due to the inclusion of map edge polygons as described above. Still, the graph for old-growth hemlock, the dominant Sylvania ecosystem type, shows higher peaks for D than all Border Lakes types (Fig. 3). If D is calculated for increasingly aggregated size

ranges, only the Sylvania old-growth hemlock has patch sizes that are significantly different across a broader range. Patch sizes surrounding the two distinct peaks in the graph ($\log(\text{Area}) < 4.6$ and $\log(\text{Area})$ 5.2–7.3) were significantly different ($P < .05$); similar tests within the individual Border Lakes forest types were not significant.

Changes in D across a range of patch sizes within an ecosystem type indicate that patch shape is a characteristic for a particular size range. This is illustrated by the three peaks in D for Sylvania hemlock (Fig. 3A), which correspond to small disturbance patches, medium-sized string-like patches surrounding wetlands and lake margins, and the large, matrix-forming patches that dominate the landscape (Pastor and Broschart

1990). The second-growth forest types on Border Lakes are characterized by less variability in D across the size classes, generally lower fractal dimensions, and a reduced patch size range, particularly in the larger sizes (Fig. 2).

DISCUSSION

Landscape structure and regional succession patterns

Our analysis has described the structure of a successional, disturbed forest landscape containing scattered old-growth patches, and compared that landscape with a nearby intact old-growth forest landscape. We suggest that similarities in structure between these landscapes relate to common landform, soils and natural disturbances, and differences between these two landscapes relate to human activities. Landscape comparisons and patch dynamics within the two study landscapes must be viewed in the context of the transitional boreal-temperate forest region in which the landscapes occur (Pastor and Mladenoff 1992). Dominant disturbance modes and frequencies differ between the boreal and northern hardwoods regions, with short return-interval fires typically regenerating boreal forests (Heinselman 1973) and catastrophic windthrow of only once a millenium common to northern hardwoods (Canham and Loucks 1984). Small treefall gaps become the most important functional patch within northern hardwoods (Mladenoff 1987, 1990), because the long disturbance intervals exceed the life-span of the dominant trees by several times (Canham and Loucks 1984).

The addition of human disturbance on the Border Lakes landscape has produced a complex of forest patches dominated by northern hardwood or boreal species, mixtures of the two, and the successional hardwoods characteristic of seres in both regions. Furthermore, human disturbance has altered patch sizes, shapes, and their spatial relationships. This disturbance-derived landscape will likely change with the convergence of the various successional pathways initiated on Border Lakes. However, moderate climate variation (Davis 1984), and continued human disturbances, even indirect impacts, such as fire suppression or sustained high deer populations (Alverson et al. 1988), may influence future forest change on Border Lakes.

Distinguishing features of the disturbed and old-growth landscapes

Our purpose in analyzing the Border Lakes and Sylvania landscapes has been to determine if there are structural characteristics that distinguish one from the other. If there are such differences, the spatial characteristics of the old-growth Sylvania landscape may be useful in setting objectives for forest landscape restoration and in modifying the management of har-

vested landscapes to enhance the natural landscape characteristics found in Sylvania. The contrasting landscape patterns we found in Sylvania and Border Lakes also can serve as hypotheses to be tested against other disturbed and primary forest landscapes. These spatial concepts can form a basis for restoring natural spatial patterns to managed forest landscapes, and may apply to other forest regions as well.

1) The range of patch size is less in the disturbed Border Lakes compared to the undisturbed Sylvania landscape. Small patches (<5 ha) are most abundant for all forest types in both landscapes. However, the large, landscape-integrating patches of old-growth hemlock that are characteristic of Sylvania are lacking on both Border Lakes old-growth remnants and successional forests. These large patches form the landscape matrix and are the major connective network on the natural landscape.

2) Large hemlock patches have the greatest fractal dimension. Where these large, complex matrix patches occur with abundant very small patches, both forest interior (habitat) and patch interspersion (connectivity) are maximized on the landscape. Additionally, only the forests of the natural Sylvania landscape have fractal dimensions that change significantly across patch size classes within a given type (Fig. 3). These differences in patch shape with size may indicate characteristic processes of patch initiation operating at different spatial scales for a given ecosystem type. The lack of such characteristic patterns in the Border Lakes landscape is another structural characteristic lost due to human disturbance.

3) There is considerable variation in patch shape and complexity between ecosystems at similar scales. This pattern suggests differential ecosystem responses to disturbance and geomorphology.

4) On the largely successional Border Lakes landscape, the greater number of forest types, their smaller and simpler patch size, and greater number of patches result in a landscape characterized by lower connectivity and thus greater habitat isolation. Additionally, much higher edge : interior ratios result in the remaining old-growth fragments and the second-growth types.

5) Characteristic juxtapositions of ecosystem patch types, e.g., old-growth hemlock adjacent to lowland conifers, are typical of the natural Sylvania landscape, and are now lacking on Border Lakes. These may be important structural characteristics that are key to both the maintenance and future restoration of hemlock on the landscape and the movement of animals between conifer stands. Successional conifer types now occupy analogous sites next to lowland conifers on Border Lakes and may be indicators of sites suitable for hemlock restoration.

6) In this heavily glaciated region, even at the landform-controlled scale the landscape is characterized by a high level of natural heterogeneity, with uplands punctuated by abundant, independently distributed

wetland and aquatic patches. Although upland forests dominate as the landscape matrix (hemlock in the natural Sylvania landscape), unbroken landscapes of old-growth forest of hundreds of hectares did not exist and therefore cannot be considered a realistic goal of landscape restoration.

7) The apparent increase in landscape diversity on Border Lakes vs. Sylvania is an artifact of human disturbance that should not be viewed as a management goal. This effect is analogous to the increase in species diversity at a local level (Ricklefs 1987) (e.g., forest stand) that can occur following disturbance. Diversity is higher on Border Lakes due to the greater number of regionally common successional types on the landscape, but at the expense of overall regional diversity (i.e., loss of less common old growth).

8) Others have suggested that human activities simplify landscape structure (Krummel et al. 1987, Turner and Ruscher 1988). However, such disturbance can increase or decrease perceived landscape heterogeneity, depending on the observed scale and the particular parameter measured. In this study, patch complexity is lower on the disturbed landscape, but there is a greater number of landscape patches and ecosystem types.

9) Within a predominantly forested landscape, habitat-level heterogeneity is largely due to differing tree species composition between patches, and structural variation due to conifer-broadleaved deciduous differences. This is fine-grained heterogeneity, since at only a slightly coarser scale the upland landscape is perceived as all forested, without a preponderance of hard patch edges between ecosystems (Forman and Godron 1986). Although forest ecosystem maps convey many discrete forest patches, the highest contrast edges and most pronounced heterogeneity in a natural landscape (Sylvania) are due to structural differences between upland forest and wetland patch types.

Summary

Protection of biological diversity should be considered in a broad landscape context that includes the vast majority of lands being used for a variety of purposes. Most reserves are ecosystem remnants of limited size. Few if any represent intact ecosystems and no single reserve can provide all ecosystem values. Increasingly, the importance of landscape context in determining the processes that occur within the boundaries of small, isolated reserves or remnant old-growth patches is being recognized (Noss 1983, 1987, 1991, Janzen 1986). The lesson from this understanding is to consider each reserve, each patch, as a functional component of a larger landscape mosaic.

Baker (1989) has noted that conservation goals at species, community, and landscape levels may actually conflict. In some cases of high disturbance and environmental heterogeneity there may not be a landscape scale at which a steady-state patch mosaic (Bormann and Likens 1979, Pickett and White 1985) or mini-

um dynamic area (Pickett and Thompson 1978) occurs. Such a pattern of landscape equilibrium, if present, would theoretically further ecosystem recovery and persistence through time. Additionally, forest ecosystems of long-lived tree species (hundreds of years) and the resulting patch structure we observe in the landscape may be more representative of past environments than those of the present (Davis and Botkin 1985), given stochastic factors and climatic variation.

In the Lake States, large reserves such as the Sylvania Wilderness also comprise the only existing examples of landscapes minimally affected by direct human activities. These reserves are our only examples of structural properties that occur in relatively intact landscapes. It is also true, however, that in many regions today, areas of old-growth remnants such as the Border Lakes landscape represent the only possible sites for restoring old-growth landscape habitat and functions. Our results suggest several attributes that differ between the disturbed, successional landscape and the Sylvania old-growth landscape, which should be considered in the design, management, and restoration of functioning old-growth ecosystems as well as the modification of management applied to larger harvested forest landscapes.

The implications of these structural changes in terms of ecological processes are not clear, but changes in structural diversity are likely to result in changes in compositional and functional diversity as well (Crow 1989). There is much to learn from old-growth landscapes that can be applied to managed landscapes (Crow 1990). A prudent first step is to mimic the complexities and characteristics of natural landscapes in our human-modified, cultural landscapes. We can use a variety of management techniques to recreate some of the patterns that characterize natural old-growth landscapes in our managed forests. Such managed commodity forests will likely continue to form the larger forest matrix. However, long-term maintenance and restoration of natural old-growth landscapes and compatible management of adjacent commodity lands requires much further research. This research will particularly address ecosystem response to natural and management disturbance, and how these processes actually relate causally to the properties and structure we have described on these landscapes.

Further work is needed both to test elsewhere for the patterns we have found and to increase our understanding of the functional and causal aspects of the patterns we have characterized. Thus far our research has quantitatively described structural pattern in two contrasting disturbed and intact forested landscapes. The structural patterns we described may be useful in designing core areas for biodiversity protection and old-growth ecosystem restoration on a landscape scale. The overall landscape context is the level that must be addressed in research and management to provide adequate ecosystem area and connectivity for animal and material

movement, species dispersal, and to facilitate the recovery of ecosystem processes in response to disturbances and successional changes. Forest landscapes both within our region and other regions should also be analyzed to determine the extent to which our results are generally characteristic of old-growth and disturbed landscapes.

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