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Ownership and ecosystem as sources of spatial heterogeneity in a forested landscape, Wisconsin, USA

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Abstract

The interaction between physical environment and land ownership in creating spatial heterogeneity was studied in largely forested landscapes of northern Wisconsin, USA. A stratified random approach was used in which 2500-ha plots representing two ownerships (National Forest and private non-industrial) were located within two regional ecosystems (extremely well-drained outwash sands and moderately well-drained moraines). Sixteen plots were established, four within each combination of ownership and ecosystem, and the land cover on the plots was classified from aerial photographs using a modified form of the Anderson (U.S. Geological Survey) land use and land cover classification system.

Upland deciduous forests dominated by northern hardwoods were common on the moraines for both ownerships. On the outwash, the National Forest was dominated by pine plantations, upland deciduous forests, and upland regenerating forests (as defined by <50% canopy coverage). In contrast, a more even distribution among the classes of upland forest existed on private land/outwash. A strong interaction between ecosystem and ownership was evident for most comparisons of landscape structure. On the moraine, the National Forest ownership had a finer grain pattern with more complex patch shapes compared to private land. On the outwash, in contrast, the National Forest had a coarser grain pattern with less complex patch shapes compared to private land. When patch size and shape were compared between ecosystems within an ownership, statistically significant differences in landscape structure existed on public land but not on private land. On public land, different management practices on the moraine and outwash, primarily related to timber harvesting and road building, created very different landscape patterns. Landscape structure on different ecosystems on private land tended to be similar because ownership was fragmented in both ecosystems and because ownership boundaries often corresponded to patch boundaries on private land. A complex relationship exits between ownership, and related differences in land use, and the physical environment that ultimately constrains land use. Studies that do not consider these interactions may misinterpret the importance of either variable in explaining variation in landscape patterns.

Introduction

Many factors account for changes in land use and the resulting patterns on the landscape. Obviously, factors such as human demographics, income, technology, political and economic institutions, and cultural conventions strongly influence how land is used (Meyer and Turner 1994; Naveh 1995; Nassauer 1995, 1997). In addition to these social and economic factors, landscape patterns are affected by physical conditions such as climate, soil productivity, and physiography. The interplay between social and economic driving factors, along with the abiotic and biotic environments, generates spatial patterns at a multitude of spatial scales (Kotliar and Wiens 1990; Milne 1991; de Roos and Sabelis 1995). Moreover, there is a strong historical element to current landscape patterns. Past land uses are reflected in the current composition and struc-

ture of a landscape (Mladenoff et al. 1993; Andersen et al. 1996; Russell 1997). These complex interactions make it challenging to elucidate the causes of spatial heterogeneity.

Our study is directed at understanding the underlying factors affecting the structure of landscapes in a largely forested region of the Lake States. The basic unit of study is a patch that typically represents a discrete and internally homogeneous entity at a given spatial scale (Kotliar and Wiens 1990). In landscapes, spatial heterogeneity can be characterized as: (1) number of patch types, (2) proportion of each cover type, (3) spatial arrangement of patches, (4) patch shape, and (5) contrast between neighboring patches (Li and Reynolds 1994). Heterogeneity, as characterized by these parameters, is a reflection of the physical environment; the imprint of past land use, as well as the effects of present land cover; and the interaction among these variables.

Our objective was to partition the sources of variation in the composition and structure of a landscape as related to the physical environment and land use as affected by ownership, and to explore the nature of their interaction on explaining landscape heterogeneity. We tested the hypotheses that both physical environment and ownership account for significant portions of the spatial variation, but that a strong interaction can confound the interpretation of their individual contribution. In this study, scale is held constant to simplify our investigation of spatial heterogeneity in a landscape.

Methods

Study site description

The study area was a 29,340-km^2 forest-dominated landscape as defined by the boundaries of the 1:250,000 U.S. Geological Survey (USGS) Ashland Quadrangle in northwestern Wisconsin, USA (Figure 1). The entire study area shares a common land-use history. In the late 1800s and early 1900s, intensive logging occurred throughout northwestern Wisconsin. Logging in combination with subsequent fire created a landscape dominated by young forests of aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and maple (*Acer spp.*) in the uplands. Following logging in the Great Lakes region, many attempts to farm marginal lands failed, resulting in tax forfeitures in the 1920s and 1930s (Flader 1983). These forfeitures constitute the source of extensive public ownership of forest land in the Lake States, including the Chequamegon National Forest. In general, however, the most prevalent process in the study area was reforestation.

Among the various ownerships (National Forest, National Park, state, county, native American, forest industry, private non-industrial) present in the study area, the Chequamegon National Forest and private non-industrial lands were selected for the study because they represent the largest holdings and they were assumed to be divergent in terms of land management practices and land use patterns.

Sampling for the study was conducted within the framework of an ecosystem classification. Ecosystems are a volumetric segment of the Earth that are defined by their atmosphere, landforms, soils, and biota. Ecosystems exist at a variety of scales, large and small, nested within one another in a hierarchy of spatial sizes (Barnes et al. 1998). Regional ecosystems were identified by using a geographic information system (GIS) and multivariate statistical analyses to integrate climatic, physiographic, and edaphic information into a classification (Host et al. 1996). Climatic regions were identified from a high-resolution climatic database consisting of 30-yr mean monthly temperature and precipitation values interpolated over a 1-km^2 grid across the study area. Principal component analysis (PCA), coupled with an isodata clustering algorithm, was used to identify regions of similar seasonal climatic trends. Maps of Pleistocene geology and major soil morphosequences were then used to identify the major physiographic and soil regions within the landscape. Climatic and physiographic coverages were then integrated to identify regional landscape ecosystems. Host et al. (1996) provide a detailed description of this approach for developing regional ecosystem classifications.

Two regional ecosystems representing different soil and physiographic conditions within a strongly continental climate were selected for our study. The first, the Copper Falls outwash, is an interlobate area that was formed from both collapsed and uncollapsed proglacial stream deposits. This regional ecosystem represents one of the most conspicuous Pleistocene landforms in Wisconsin, the spillway of Glacial Lake Superior, and it is now the drainage for the St. Croix and Brule Rivers (Albert 1995). Before European settlement, these landforms were barrens of jack pine (*Pinus banksiana*) and northern pin oak (*Quercus ellipsoidalis*) along with scattered red pine (*Pinus resinosa*). Current vegetation has been

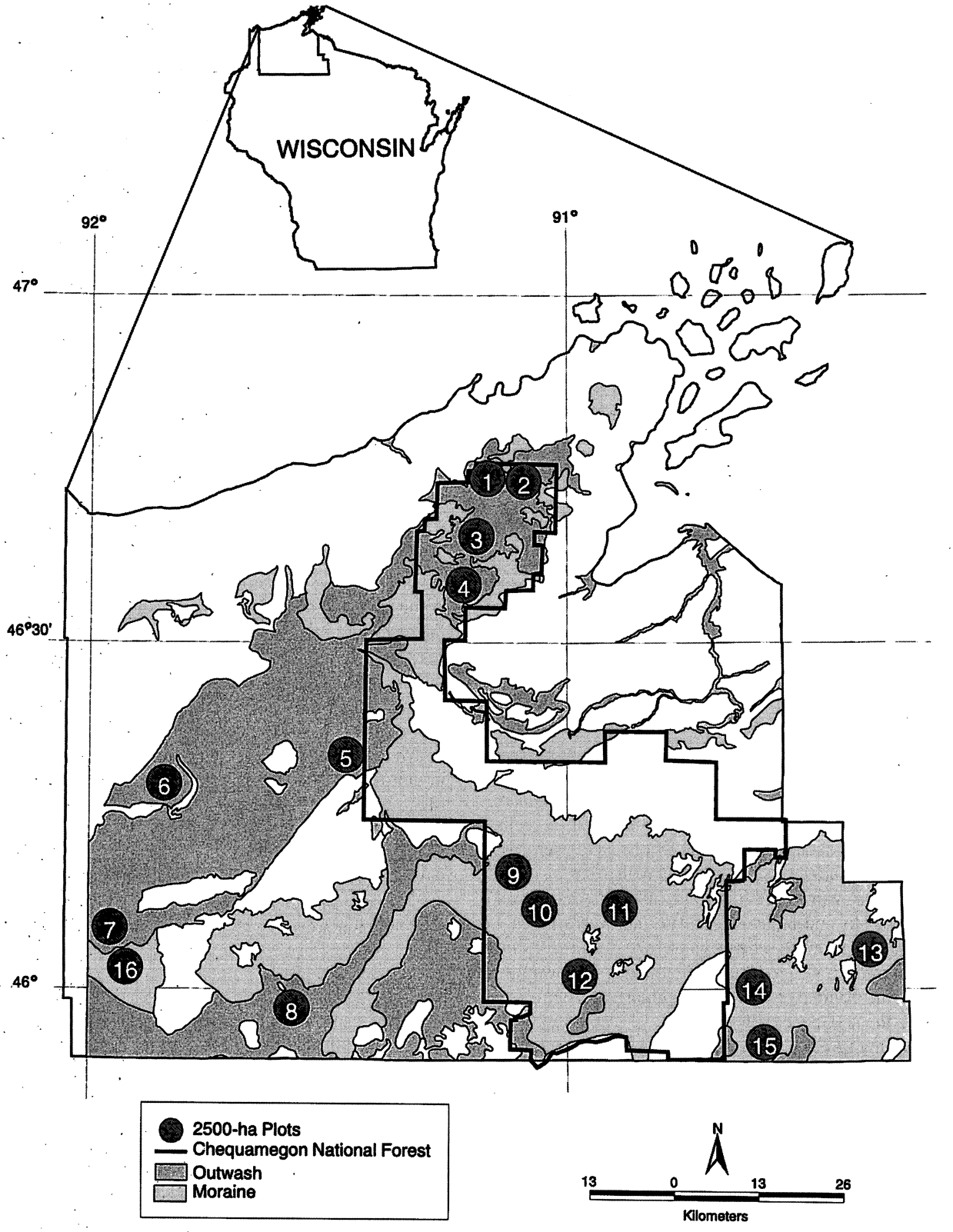

Figure 1. Map of study area in northwestern Wisconsin showing location of study plots within the outwash and moraine ecosystems. The boundary of the Chequamegon National Forest is also shown. Plots located outside this boundary are on private non-industrial land.

greatly modified by fire suppression and the conversion of pine barrens to plantations. The second regional ecosystem, the Copper Falls moraine, developed from mass-movement tills that were deposited to various depths following glacial retreat and then covered by windblown loess (Clayton 1984). The vegetation is largely mesic northern hardwood forests dominated by sugar maple (*Acer saccharum*), eastern hemlock (*Tsuga canadensis*), yellow birch (*Betula alleghaniensis*), with white pine (*Pinus strobus*) and red pine. Forested wetlands occupied by northern white-cedar (*Thuja occidentalis*), black ash (*Fraxinus nigra*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*) are also common. For ease of reference, the two regional ecosystems subsequently will be referred to as outwash and moraine in this paper. The outwash regional ecosystem corresponds to Albert's (1995) Bayfield Barrens (Subsection X.1) classification unit; the moraine regional ecosystem is within the Upper Wisconsin/Michigan Moraines (Subsection IX.3).

Plot establishment

The first step in establishing sample plots was to produce three ARC/INFO (Environmental Systems Research Institute, Redlands, CA) coverages for the northwestern portion of Wisconsin: one of land ownership, a second of regional ecosystem boundaries, and a third of land cover obtained from USGS LUDA digital data. Each was rasterized to a grid-cell size of 100 × 100 m (1 ha) to produce grids containing 1400 rows and 1700 columns.

Two new grid coverages were then extracted from the original ownership coverage. In the first, all cells that corresponded to National Forest land were assigned a value of one and all other cells were assigned a value of zero. In the second, all cells that corresponded to non-industrial private land were given a value of one and all other cells were set to zero. A similar approach was used to extract new grid coverages from the original coverage of regional ecosystems and from the land cover (LUDA).

Using ARC/INFO's raster processing module GRID, we generated new grids on the two ownership coverages where the value in each cell was the sum of the values for all the grid-cells within a 29 cell (2800 m) radius. Each grid-cell was 1 ha in area, so the value assigned each cell in the output grid was the area of land (National Forest in the first output grid, private non-industrial land in the second output grid) within a 2500-ha circular plot centered on that grid-cell. The same operation was also applied to generate output grids for the regional ecosystems (outwash and moraine) and one output grid of upland forest within a radius of 2800 m. Using these five grid coverages in combination, we determined the areas of National Forest, private non-industrial land, outwash, moraine, and upland forest for the entire study area.

Four final grids were generated by selecting those cells that were: (1) entirely within the outwash ecosystem, but at least 90% National Forest land and at least 75% upland forest; (2) entirely within the outwash ecosystem, but at least 90% private non-industrial ownership and at least 75% upland forest; (3) entirely within the moraine ecosystem, but at least 90% National Forest land and at least 75% upland forest; and (4) entirely within the moraine ecosystem, but at least 90% private non-industrial ownership and at least 75% upland forest. The number of cells in each grid that satisfied the criteria ranged between 1256 and 3763, and these cells generally formed from one to seven clusters in each grid. Random numbers were listed for each grid-cell, and the list was sorted in ascending order. Eighty circles with a radius of 2800 m each were generated using the coordinates for the first 20 randomly selected cells listed for each grid. From those, the first four non-overlapping circles in each grid were selected as sample plots to be used for the study (Figure 1). The result is a stratified random design with a two × two matrix for ownership and ecosystem and four replications for each combination.

We used a previous study of landscape pattern in northern Wisconsin to help establish plot size. Mean patch size in classified aerial photography from Mladenoff et al. (1993) stabilized at about 10 km^2. An even larger plot size (25 km^2) was selected to reduce the likelihood that measures of patchiness would be significantly biased from the truncation of polygons by plot boundaries.

Photo interpretation

The composition and structure of the landscape were documented from aerial photography flown during the summer and fall of 1993. The photographs were 1:15840 black and white infrared or 1:12000 natural color. The land cover was interpreted and delineated onto estar-base film and the class boundaries were transferred and rectified to 1:24000 scale USGS topographic maps using a zoom transfer scope. We then manually digitized these boundaries into PC

Table 1. The hierarchical classification used to characterize land cover in the study area. Also included are the number of polygons checked in the field and the percent of polygons with the correct classification in the photo interpretation. Class 3.0 (water) includes lakes, streams. Class 5.0 (non-agriculture) represents open lands other than agricultural areas (i.e., housing, road and utility right-of-ways, gravel pits and other disturbed areas, barrens).

Level	Description	Correct classification (%)	Sample number of polygons
1.0	Agriculture	92	13
1.1	Cropland	100	10
1.2	Pasture	67	3
2.0	Forest	98	225
2.1	Upland deciduous	93	42
2.2	Upland coniferous	57	23
2.3	Upland mixed	80	87
2.4	Regenerating forest	91	46
2.5	Plantations	67	27
3.0	Water	100	7
4.0	Wetlands	94	127
4.1	Wetland deciduous	71	21
4.2	Wetland coniferous	93	45
4.3	Wetland mixed	80	5
4.4	Nonforested	82	38
4.5	Regenerating forest	78	18
5.0	Non-agriculture	80	10

ARC/INFO software and attached labels representing a cover class to the polygons.

We used a modified Anderson et al. (1976) level I and II classification for land cover. Level I classes included agriculture, forest, water, wetlands, and non-agricultural open lands (Table 1).

At level II, agricultural lands consisted of cropland and pasture (Table 1). Old fields with trees were still considered pasture if canopy coverage was $\leq$50%. Fallow land once used for agriculture but remaining in grass cover was considered agricultural land and was classified as pasture. As established by Anderson's classification, both upland and lowland mixed forests were composed of $\geq$33% but $\leq$67% (canopy coverage) mixtures of coniferous and deciduous species. At higher or lower mixtures, stands were classified as conifer or hardwood forests. Classification of regenerating forests was based on <50% canopy coverage. Non-agriculture open lands included housing, road and utility rights-of-ways, disturbed areas such as gravel pits, and brushy and barren areas. The minimum polygon size recognized in the classification of the aerial photography was 1.0 ha for upland patches and 0.5 ha for wetland patches. The difference in minimum size allowed more of the small wetlands embedded in the upland matrix to be included in the land cover classification.

A total of 10% of the classified polygons from each plot were field checked. Polygons were selected for field checks in proportion to the frequency of their classification. Accuracy of the classification exceeded 90% in four of the five level I classes and for many level II classes (Table 1). Among the exceptions at level II were Upland Coniferous (2.2) and Plantations (2.5). Because mature plantations that had been thinned several times were difficult to distinguish on the aerial photographs from natural stands of upland conifers, these two cover classes were sometimes improperly classified.

Analysis

Comparisons of landscape composition and structure derived from the classification of the 1993 aerial photographs were made among plot sets, each replicated four times:

- Plot set I – National Forest, outwash;
- Plot set II – private non-industrial, outwash;
- Plot set III – National Forest, moraine;
- Plot set IV – private non-industrial, moraine.

We applied the vector version of the software program FRAGSTATS (McGarigal and Marks 1995) to quantify landscape structure for the level II classification. When plot size is held constant, as in our study, the number of patches conveys the same information as unit area measurements such as patch density; therefore, we report only number of patches by plot. An area metric, the largest patch index which quantifies the percentage of each plot comprised by the largest patch, was included because large patches represent an important structural element in the landscape (Mladenoff et al. 1993). The largest patch was defined entirely within the boundaries of the 2500-ha sample plot. Three additional metrics used to characterize landscape structure are landscape shape index, Shannon's diversity index, and an interspersion and juxtaposition index (IJI). The shape index is a measure of the perimeter-to-area ratio. A more complex shape will have a higher ratio than a less complex shape. Shannon's diversity index increases as the number of patch types increases or the proportional distribution of area among patch types becomes more equitable, or

both (McGarigal and Marks 1995). The interspersion and juxtaposition index quantifies landscape configuration. Each patch is evaluated for adjacency with all other patch types. This index measures the extent to which patch types are interspersed, with the highest value (IJI = 100) occurring when the corresponding patch type is equally adjacent to all other patch types (McGarigal and Marks 1995). We tested for statistical differences among the metrics using analysis of variance in the GLM Procedure from SAS (SAS Institute Inc. 1988).

Distributions of patch size-classes were also used as a measure of landscape structure. Areas for all patches for a size class were summed where the classes represented a geometric series of patch sizes ($class_1$ = 0.1–2.0 ha, $class_2$ = 2.1–4.0 ha, $class_3$ = 4.1–8.0 ha...). To test the hypothesis that two or more groups of observations have identical distributions, we used the Kolmogorov-Smirnov statistic to perform analysis of variance on ranks using several statistics based on a empirical distribution function (SAS Institute Inc. 1988).

Results

Landscape composition

By design, upland forest dominated all four plot sets (Figure 2). The percentage of upland forest ranged from an average of 95% of the total area for National Forest on outwash to a minimum of 64% for National Forest on moraine. The two private/ecosystem plot sets each averaged 65% of their total area in upland forest. The percentage of upland forest fell below the threshold of 75% coverage required for plot establishment because the resolution used for classifying the aerial photographs was higher than the resolution of the LUDA data used for establishing plot locations.

There were differences among plot sets for the other level I cover classes (Figure 2). A higher proportion of private land on outwash was in water (8%) compared to the other plot sets (areas surrounding large lakes on the outwash stayed in private ownership), but water accounted for a small proportion of the total area. As expected, private land had greater amounts of agricultural land (4 and 7%) than did public land (<1%). Also, wetlands occupied a larger percentage of the landscape on moraine (25 and 32%) compared to outwash (<1 and 8%), and non-agricultural open lands were more common on outwash than on moraine (Figure 2).

Additional information about the composition of the landscape can be gained from the level II classification (Table 2). The National Forest plots on outwash (Plot Set I) were dominated by plantations, upland deciduous forest, and upland regenerating forest. Combined, these three cover classes accounted for 54% of the patches and 85% of the total area. Plantations alone accounted for 41% of the total area. Many small patches of upland mixed (coniferous and deciduous species) existed on the outwash ecosystem on National Forest ownership. The average patch size for upland mixed forest was 4.5 ha, compared to 23.0, 14.5 and 30.6 ha for upland deciduous, upland regenerating forest, and plantations, respectively. A more even distribution among the classes of upland forest is evident for private land on outwash (Plot Set II), where much less of the total area was in regenerating forest and plantation compared to public land (Table 2). Upland deciduous forests dominated by sugar maple were common to the moraine ecosystem for both ownerships. Among the four plot sets, private land on outwash had the highest representation of non-agriculture open lands comprised of housing, road and utility-rights-of-ways, disturbed areas such as gravel pits, brushy and barren areas.

For National Forest (Plot Set III) and private land (Plot Set IV) on moraines, upland deciduous forest accounted for 31 and 43% of the total area, respectively (Table 2). Regardless of ecosystem, plantations represented a much larger share of the landscape matrix on public land compared to private land. As previously noted, most wetlands were small inclusions in the upland matrix as suggested by the higher values for percent patches than for percent area (Table 2). The prevalence of upland forest throughout our study area established a common matrix for comparing landscape structure.

Landscape structure

Significant differences ($P<0.01$, Kolmogorov–Smirnov test) in landscape structure existed by ownership and ecosystem. On outwash, private land consistently had a higher representation of smaller patches than did public lands for the combination of all cover classes (Figure 3a). If patch-size distributions are accepted as a measure of fragmentation, then private land was more fragmented than public land on outwash. The opposite was true for the moraine ecosystem (Figure 3b). In this case, public land had a greater representation

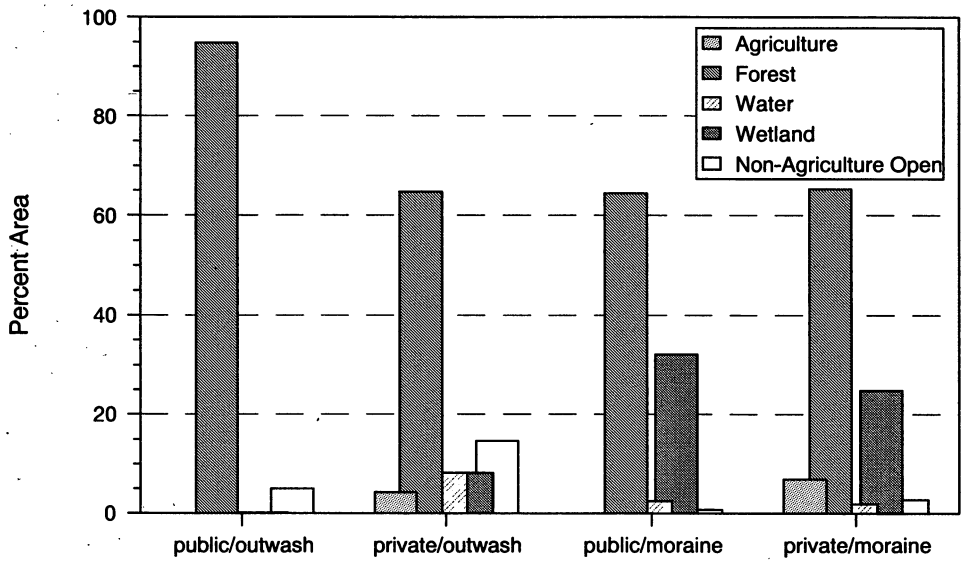

Figure 2. The percent of total area in agriculture, forest, water, wetland, and non-agricultural open land. Based on four 2500-ha plots for each set.

in smaller patch size-classes, creating a finer grain to landscapes on public than private land.

When ownership was held constant and ecosystem varied, a different pattern was observed. Although significant differences ($P<0.01$) in size-class distributions between ecosystems were present on public land (Figure 4a), there were no significant differences ($P>0.05$) in landscape patch-size distributions between ecosystems on private land (Figure 4b). Also, note the lack of representation in the largest patch size-class on private land (Figures 3a, 3b, 4b). This important structural element of a landscape is missing on private land in our study plots.

Further insights about landscape structure can be obtained by considering mean patch size among the plot sets and by level I land cover classes (Table 3). For upland forest, the most prevalent cover class, the trends for mean patch size among the plot sets parallel the distributions of patch size in Figures 3 and 4. The largest mean patch size is found on National Forest land on outwash, while the smallest mean patch size is found on National Forest land on moraine (Table 3). The differences in mean patch size for upland forest were not significantly different by ownership ($MS = 3.276$, $F = 2.59$, $P = 0.108$) or ecosystem ($MS = 3.835$, $F = 3.03$, $P = 0.082$), but the interaction between ownership and ecosystem was highly significant ($MS = 27.811$, $F = 21.97$, $P < 0.001$).

Somewhat different patterns emerged for other cover classes. Patches of water on private land, especially on the outwash ecosystems, tended to be larger than those on public land (Table 3). These differences were statistically significant ($MS = 11.004$, $F = 6.02$, $P = 0.016$), but differences in mean patch size for water were not different by ecosystem ($P = 0.912$), nor was the interaction term in the linear model significant ($P = 0.167$). Only 0.2% of the area on National Forest on outwash was classified as lakes, streams, and reservoirs, compared to 8.2% for private land on outwash (Table 2). Not only were there smaller patches of water on average on public land compared to private land, but there were also fewer patches.

Wetland, including both forested and nonforested wetlands, tended to be more frequent and larger on the moraine ecosystem than on the outwash (Tables 2 and 3). Not surprisingly, the physical environment or ecosystem accounted for the largest share of the variability ($MS = 27.390$, $F = 30.95$, $P < 0.001$). The interaction term was also significant ($MS = 10.570$, $F = 9.88$, $P = 0.002$), but differences by ownership were not ($P = 0.331$).

Unlike wetlands that are products of the geomorphological features of the landscape, the nonagriculture cover class is a result of anthropogenic activities. The variety of land uses included in this cover class produced much larger average patch size on private land than on public land (Table 3). Neither differences by ecosystem nor the interaction between ecosystem and ownership was statistically significant ($P>0.05$). The representation of agricultural lands on

Table 2. Summary of landscape metrics for the Level II land classification. Each value is based on four sample plots.

Class	Number Patches	Percent patches	Mean patch size (ha)	Area (ha)	Percent area	Number Patches	Percent patches	Mean patch size (ha)	Area (ha)	Percent area
Plot Set I – National Forest; outwash						Plot Set II – Private; outwash				
Cropland						40	3.8	9.2	369.1	3.71
Pasture						9	0.9	6.3	6.5	0.57
Upland deciduous	101	14.4	23.0	2321.6	23.34	110	10.5	16.3	1790.3	18.00
Upland coniferous	37	5.3	3.9	143.4	1.44	105	10.0	6.2	650.2	6.54
Upland mixed	183	26.1	4.5	831.9	8.36	233	22.3	8.2	1907.2	19.17
Regenerating forest	144	20.6	14.5	2093.2	21.04	115	11.0	7.1	819.8	8.24
Plantations	132	18.9	30.6	4033.8	40.55	90	8.6	14.2	1274.3	12.81
Lakes, streams, reservoirs	8	1.1	2.0	15.9	0.16	50	4.8	16.3	816.4	8.21
Wetland deciduous						21	2.0	8.0	168.1	1.69
Wetland coniferous	4	0.6	1.3	5.1	0.05	40	3.8	2.3	92.3	0.93
Wetland mixed						34	3.3	1.9	65.5	0.66
Nonforested	15	2.1	0.8	11.7	0.12	137	13.1	3.5	474.9	4.77
Regenerating forest						9	0.9	1.0	9.3	0.09
Non-agriculture open land	76	10.9	6.5	492.3	4.95	53	5.1	27.4	1454.5	14.62
Total	700		14.2	9948.2		1046		9.5	9948.2	
Plot Set III – National Forest; moraine						Plot Set IV – Private; moraine				
Cropland						78	6.9	6.6	517.8	5.21
Pasture	1	0.1	1.6	1.6	0.02	34	3.0	5.2	177.0	1.78
Upland deciduous	153	11.0	20.1	3076.5	30.93	127	11.3	34.1	4327.3	43.50
Upland coniferous	116	8.4	4.9	570.9	5.74	40	3.6	4.4	174.4	1.75
Upland mixed	252	18.1	5.6	1406.4	14.14	194	17.2	7.3	1412.1	14.19
Regenerating forest	94	6.8	4.1	388.2	3.90	91	8.1	5.1	465.3	4.68
Plantations	93	6.7	10.5	973.9	9.79	21	1.9	5.3	111.1	1.12
Lakes, streams, reservoirs	41	3.0	6.1	251.8	2.53	28	2.5	7.0	194.7	1.96
Wetland deciduous	49	3.5	2.5	121.4	1.22	51	4.5	5.6	283.9	2.85
Wetland coniferous	239	17.2	5.8	1388.5	13.96	129	11.5	5.8	742.4	7.46
Wetland mixed	109	7.8	3.4	375.0	3.77	124	11.0	3.9	483.8	4.86
Nonforested	212	15.3	6.1	1289.5	12.96	188	16.7	5.0	930.5	9.35
Regenerating forest	16	1.2	2.0	31.5	0.32	12	1.1	2.7	32.3	0.32
Non-agriculture open land	14	1.0	5.2	73.0	0.73	8	0.7	12.0	95.8	0.96
Total	1389		7.2	9948.2		1125		8.8	9948.2	

public ownership was insufficient to justify comparisons.

We also compared mean patch size between ownership and ecosystem for the level II cover classes. Those for the most common classes – upland deciduous forest, upland mixed forest, upland regenerating forest, and plantation – are reported in Table 4. Mean patch size for upland deciduous forests, a common cover class throughout the study area, did not differ significantly either by ownership ($P = 0.171$) or ecosystem ($P = 0.111$). These comparisons, however, were confounded by a strong interaction between ownership and ecosystem ($P<0.001$) and a large mean value for a single plot. Mean patch size for upland deciduous forests averaged 99.3 ha for one plot in the public/moraine set, compared to a range of 6.6

Table 3. Mean patch size for level I land cover classes by plot set and ANOVA results for P<0.05 using logarithmic transformation of patch size.

Classification	Mean patch size (ha)				ANOVA		
	NF-outwash	Private-outwash	NF-moraine	Private-moraine	Source of Variation	P value	F
Agriculture	–	8.69	1.57	6.20			
Forest	15.79	9.87	9.06	13.72	Ownership × ecosystem	P<0.001	F = 21.97
Water	1.98	16.33	6.14	6.95	Ownership	P = 0.016	F = 6.02
Wetland	0.88	3.36	5.13	4.91	Ecosystem	P<0.001	F = 30.95
					Ownership × ecosystem	P = 0.002	F = 9.88
Non-ag open	6.48	27.44	5.21	12.01	Ownership	P<0.001	F = 39.56
Combined	14.21	9.51	7.16	8.84			
Total sample size	700	1046	1389	1125			

Table 4. ANOVA results for the dependent variable of mean patch size and selected level II land cover classes.

Source	DF	Mean Square	F Value	P>F
Upland deciduous forest				
Ownership	1	3.20	1.88	0.171
Ecosystem	1	4.34	2.54	0.111
Ownership × ecosystem	1	30.74	18.02	<0.001
Upland mixed forest				
Ownership	1	18.46	21.54	<0.001
Ecosystem	1	3.57	4.16	0.042
Ownership × ecosystem	1	1.39	1.62	0.204
Upland regenerating forest				
Ownership	1	2.08	2.03	0.155
Ecosystem	1	21.17	20.68	<0.001
Ownership × ecosystem	1	15.66	15.29	<0.001
Plantation				
Ownership	1	3.62	2.18	0.141
Ecosystem	1	16.60	9.97	0.002
Ownership × ecosystem	1	0.01	0.00	0.977

to 53.8 ha for the other 15 plots. When the outlier is ignored, mean patch size for upland deciduous forests on the moraine was substantially smaller on pubic land compared to private land.

Mean patch size for upland mixed forest was significantly smaller on public than on private land (P<0.001), while differences between ecosystems were only marginally significant (Table 4). The smaller mean patch size was consistent with the broader trend of a finer grain structure for upland forests on National Forest compared to private land.

Regenerating forests were those young stands with <50% canopy coverage. In the uplands, mean patch size for regenerating forests varied strongly by ecosystem (P<0.001), but not by ownership (P = 0.155). Patches of regenerating forest tended to be larger on outwash than on moraine (Table 2). Again, there was a significant interaction between the main variables in the ANOVA (P<0.001).

Plantations were more frequent and larger on the outwash than on the moraine ecosystem (Table 4). This trend was especially obvious on public ownership, where pine plantations averaged 47.4, 57.7, 13.8, and 18.1 ha for sample plots on outwash compared to 15.3, 8.4, 11.1 and 9.1 ha in size for plots on the moraine ecosystem.

Other structural parameters varied greatly between ecosystems in public ownership. Among the four plot sets, the high and low mean values for patch number, landscape shape indices, and Shannon's diversity index were on the National Forest (Table 5). That is, National Forest land had either higher or lower patch density, complexity of patch shape, and patch diversity compared to private land, depending on the ecosystem. The largest patch index and the interspersion and juxtaposition index paralleled this trend. In spite of plot 9 where the largest patch represented 32.9% of the total plot area, the National Forest on outwash (plots 1–4) averaged 16.4% for the largest patch index compared to 10.1 to 13.0% for the other plot sets. Given this trend, it is not surprising that landscapes on National Forest/outwash had the lowest interspersion and jux-

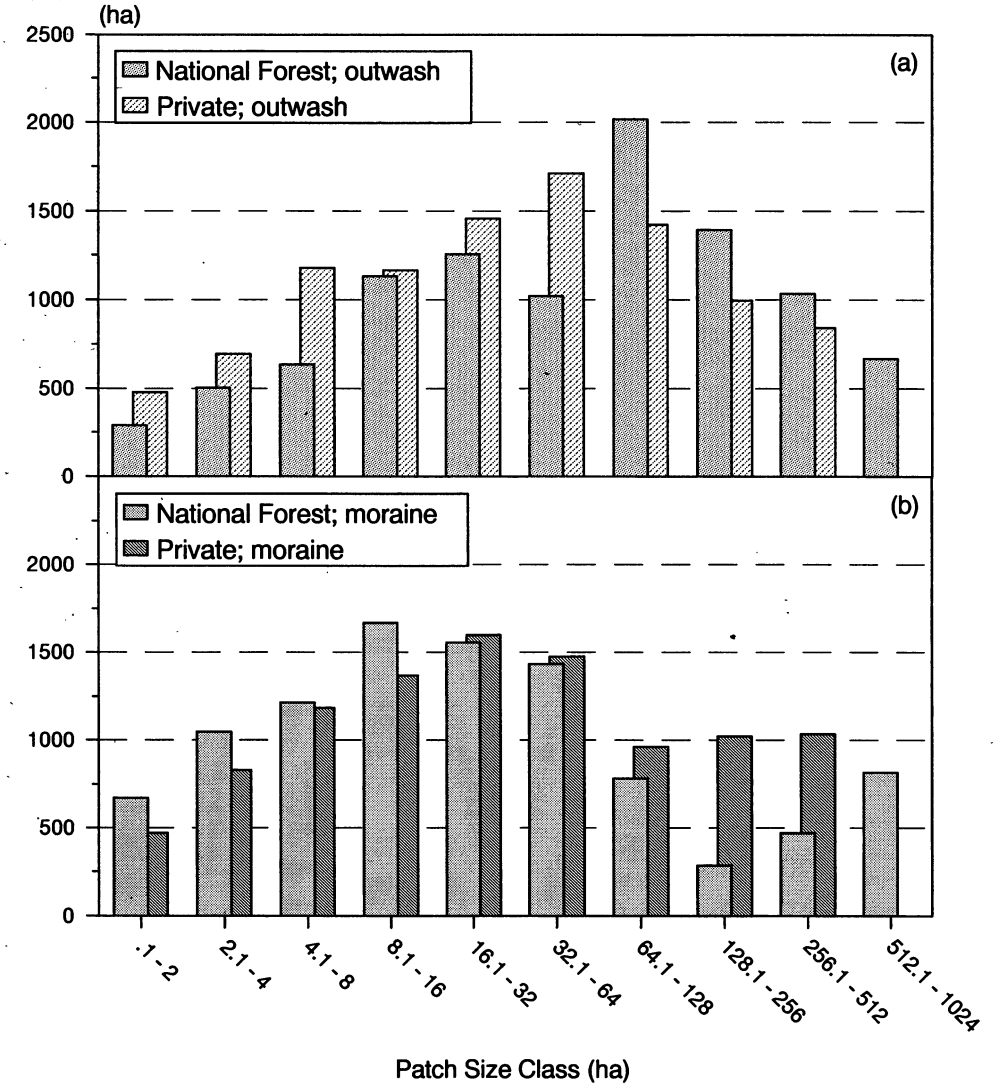

Figure 3. Comparison of patch size-classes between public and private lands on the (a) outwash and (b) moraine ecosystems. Each class represents a summation of area for all patches in each size class.

taposition (Table 5). The relative differences in these metrics for the National Forest plots on outwash and the other plot sets are striking. Both the composition of the landscape and its structure are greatly simplified compared to the other combinations of ownership and ecosystem.

In contrast to the structural parameters for National Forest land, those for private land did not vary substantially by ecosystem (Table 5). For example, the mean number of patches per 2500-ha plot on private/outwash was 262 compared to 281 for private/moraine, and Shannon's diversity index ranged only from 1.71 to 2.10 on the private land (Table 5).

Despite this trend of similar landscape structure across different ecosystems on private land, analysis of variance for number of patches, landscape shape index, Shannon's index, and interspersion/juxtaposition suggest that ecosystem accounts for larger portions of variation in these indices than does ownership (Table 6). The H_0 that no differences in number of patches, complexity of shape, or patch diversity exist was accepted for all cases except for patch diversity, which was rejected at a marginal level (P=0.04). The same H_0, however, was rejected for ecosystem except for the index of interspersion and juxtaposition (Table 6). The interpretation of these results is con-

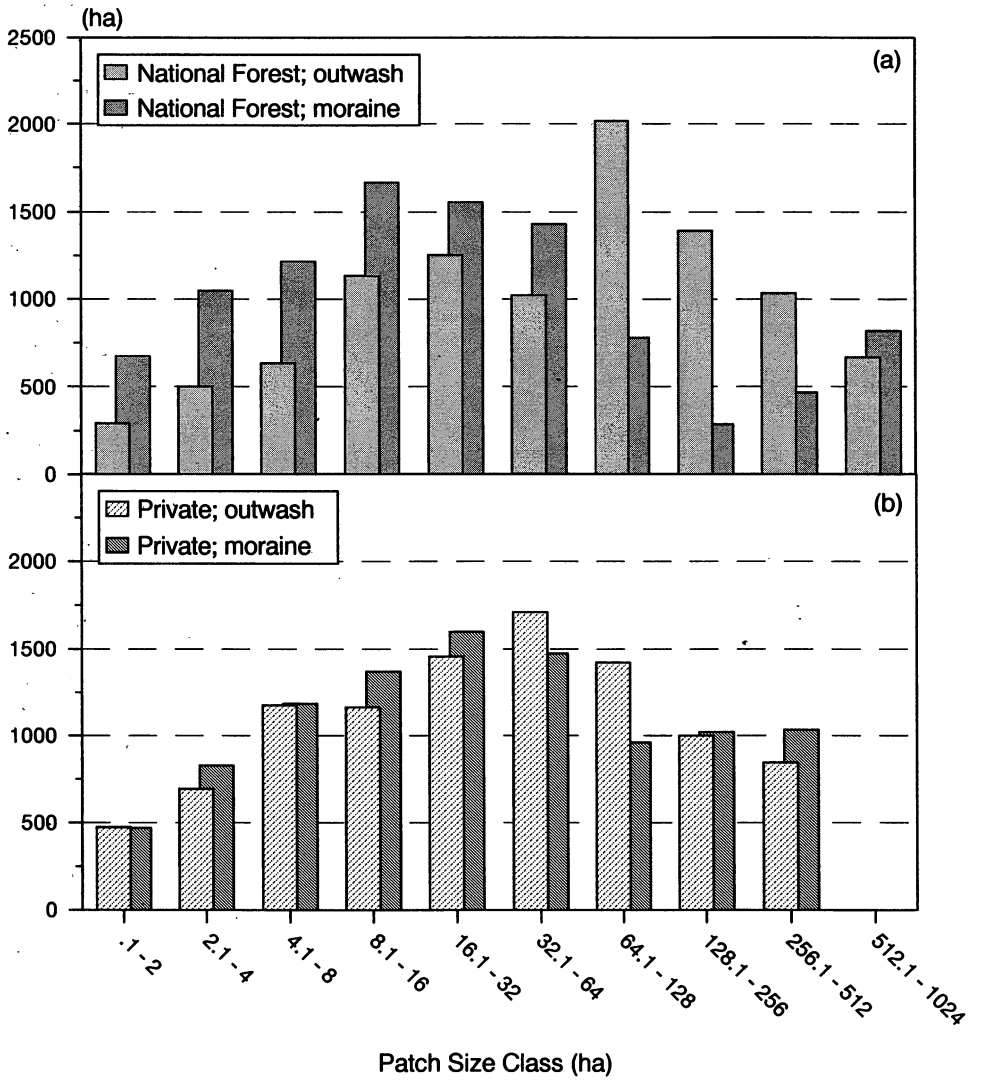

Figure 4. Comparison of patch size-classes between outwash and moraine ecosystems on (a) public and (b) private lands. Each class represents a summation of area for all patches in each size class.

founded somewhat by the significant interaction terms for the number of patches and Shannon's Diversity Index (P=0.039 and P=0.038, respectively). Clearly, the physical environment is a strong source of variation as measured by the structural indices, but it is also clear that these patterns are being greatly modified by human land-use.

Discussion

Patterns of land use reflect a complex set of interactions among social and economic factors, land uses, and environmental conditions (Brouwer 1989; Mladenoff et al. 1993; Nassauer 1995; Naveh 1995; Wear et al. 1996). In our study, we attempted to minimize the influence of land cover in the experimental design by studying landscapes that were predominately in forest cover. Further, we attempted to simplify the design by studying landscape pattern at the same spatial scale (1:24,000) and by considering conditions at a single period of time (1993). In contrast, we attempted to maximize differences in the physical environment by locating study sites on extremely well-drained outwash and moderately well-drained moraine within a similar climatic regime, and attempted to maximize the differences in land use by comparing public land (Chequamegon National Forest) to private

Table 5. Summary of landscape metrics for plots and plot sets.

	Number of patches	Patch size CV (%)	Largest patch index (%)	Landscape shape Index	Shannon's diversity index	Interspersion/ juxtaposition
National Forest–Outwash						
Plot 1	164	370.1	26.8	10.44	1.27	63.7
2	121	206.6	10.6	10.17	1.08	41.0
3	227	248.8	8.0	12.39	1.49	65.3
4	188	318.4	20.3	10.89	1.60	81.1
$\bar{x} \pm$ SE =	175±22.2	286.0±36.3	16.4±4.3	10.97±0.50	1.36±0.12	62.8±16.5
Private–Outwash						
Plot 5	204	241.8	12.9	11.87	1.75	67.3
6	248	286.3	10.7	11.09	1.83	76.8
7	253	191.8	6.2	13.33	1.71	60.4
8	341	251.1	10.4	15.20	2.10	75.8
$\bar{x} \pm$ SE =	262±28.7	242.8±19.5	10.1±1.4	12.87±0.90	1.85±0.09	70.1±3.9
National Forest–Moraine						
Plot 9	197	536.6	32.9	10.39	1.43	71.2
10	399	189.1	4.3	16.50	2.08	82.0
11	374	173.4	5.9	17.12	2.06	76.0
12	419	172.9	3.7	17.62	2.04	77.6
$\bar{x} \pm$ SE =	347±50.9	268.0±89.6	11.7±7.1	15.41±1.69	1.90±0.16	76.7±2.2
Private–Moraine						
Plot 13	262	226.3	11.6	12.94	1.95	75.5
14	246	345.9	19.4	12.58	1.85	75.3
15	309	261.7	10.8	13.25	1.80	75.5
16	308	261.4	10.1	14.64	1.91	73.8
$\bar{x} \pm$ SE =	281±16.1	273.8±25.4	13.0±2.2	13.35±0.45	1.88±0.03	75.0±0.4

(non-industrial) land. And we assumed that landscape patterns resulting from different ownerships and different land management objectives would be reflected as sources of variation in our ANOVA. These sources of variation could conceivably take several forms. Differences in landscape pattern might result from different sets of social and economic factors being considered in decision making, or the same set of factors could be considered but with different levels of importance being assigned to them.

Not surprisingly, the physical environment proved to be a strong source of spatial heterogeneity in our comparisons of landscape pattern between outwash and moraine. Differences in landscape pattern could also be attributed to ownership, but the effects of the two variables in the ANOVA model were not independent. Significant interactions between the two main variables in our model, environment and ownership, were present in many of our analyses. It is impossible to make an unequivocal statement about public or private landscapes having more or less structural complexity based on patch density, or any other measure of pattern without first qualifying the statement by the type of ecosystem under consideration. Classifications of landscape ecosystems such as those developed by Albert et al (1986), Albert (1995), and Keys and Carpenter (1995) provide a useful framework for evaluating landscape patterns.

Although the physical environment provides the ultimate constraint for land use, there is considerable variation in landscape pattern within an ecosystem caused by past and present human activities (Mladenoff et al. 1993; Andersen et al. 1996; Russell 1997). Wear and Flamm (1993), for example, found the like-

Table 6. Two-way analysis of variance of landscape metrics using log transformations of dependent variables and type II sums of squares.

Source	DF	Mean square	F Value	P>F
Dependent variable: number of patches				
Owner	1	0.0555	0.88	0.367(ns)
Ecosystem	1	0.5691	8.99	0.011(*)
Owner × ecosys	1	0.3413	5.39	0.039(*)
Error	12	0.0633		
Dependent variable: Shannon's diversity index				
Owner	1	0.0976	5.29	0.040(*)
Ecosystem	1	0.1254	6.80	0.023(*)
Owner × ecosys	1	0.1001	5.43	0.038(*)
Error	12			
Dependent variable: landscape shape index				
Owner	1	0.0010	0.04	0.837(ns)
Ecosystem	1	0.1318	5.64	0.035(*)
Owner × ecosys	1	0.0777	3.32	0.093(ns)
Error	12			
Dependent variable: interspersion/juxtaposition				
Owner	1	0.013	0.52	0.483(ns)
Ecosystem	1	0.091	3.69	0.079(ns)
Owner × ecosys	1	0.024	0.98	0.341(ns)
Error	12			

lihood of forest cover being altered was related to (1) ownership, (2) environmental factors such as slope and elevation, and (3) to geographic variables such as distance to roads and distance to market centers. In comparative studies in the southern Appalachians and Washington's Olympic Peninsula, Turner et al. (1996) did not find major differences in landscape patterns between private and public lands under commercial forest management, but there were differences in landscape composition and structure between public and noncommercial private lands. In both regions, private lands had less forest cover and greater numbers of small forest patches compared to public lands.

Significant historic events occurring in our study area that can be related to differences in landscape structure between ownerships include the conversion of large areas of tax delinquent land from private to public ownership in the 1920s and 1930s in the Lake States; the conversion of substantial areas of pine barrens, cutover and burned lands to pine plantations on public lands, especially on the outwash ecosystem as part of the social programs (e.g., Civilian Conservation Corps) during the 1930s; and the synchronous maturation of these plantations during the 1990s. As a result, large blocks of mature plantation are now being harvested on the National Forest and the outwash ecosystem, with new plantations established, or in some areas, fire has been reintroduced to restore pine barrens (Parker 1997). In effect, utilizing large harvest units and reintroducing fire on the outwash ecosystem are retaining the coarse-grained pattern of spatial heterogeneity that existed on this landscape.

Historical disturbance regimes differ on the outwash and moraine ecosystems in our study area. On moraines, windthrow is the most important natural disturbance. Although large-scale catastrophic windthrows (e.g., 1000s of ha) do occur, such disturbances are infrequent over much of the northern hardwood region of North America (Frelich and Graumlich 1994). Small windthrows that create a fine-grain pattern on the landscape are far more frequent (Runkle 1982). On the outwash, in contrast, fire is the most important disturbance factor (Heinselman 1973, Whitney 1986). Historically, fires occurred frequently, with some affecting large areas, and both large and small fires were important in maintaining the conifer-dominated upland forests (Curtis 1959). Starting in the 1930's, fire suppression greatly reduced the effect of this disturbance on landscape composition and structure. Although fires are still frequent on xeric outwash ecosystems, they are effectively contained to small areas. The lack of significant differences in many of the structural parameters between the outwash and moraine on private lands suggests that the structure of these landscapes has converged through time. If this homogenization of landscape structure is real, fire suppression is one possible explanation for the trend.

It is possible that selection bias accounted for some differences in our results. Although farming was never a common land use in the study area, ownership could be determined to some degree by the ecological capability of the land within the moraine and outwash ecosystems. For example, the most marginal lands could be in public ownership because they failed to support farming. There is some evidence to support this argument. Wetland coniferous and nonforested wetlands were slightly more common on public than private land on the moraine (Table 2). Another obvious selection factor is related to the retention in private ownership of land near large lakes on the outwash ecosystem.

An important structural element of the landscape – large natural–vegetation patches – is missing from private land and to some extent from public land. Large patches serve important ecological roles and provide many benefits in a landscape (Mladenoff et al. 1993;

Forman 1995a). Large patches provide structural connectivity within the landscape, and when large patches occur in a landscape, both interior habitat and patch interspersion (connectivity) are maximized. Due to the structural and functional importance of large patches, Forman (1995b) recommended an aggregation-with-outliers strategy for landscape design in which large patches of land use are supplemented with small patches and corridors of different land use to ensure the retention of large patches in human-dominated landscapes. Retention of large patches should be a primary goal in land management on public lands.

While characterizing environmental heterogeneity remains an important goal for many ecological studies (e.g., Krummel et al. 1987; Kotliar and Wiens 1990; Levin 1992; Li and Reynolds 1995), greater emphasis is now being placed on understanding the ecological implications of this heterogeneity. Much of this attention has been on the relation of population dynamics to spatial heterogeneity and landscape structure (Wiens 1976; Hassell 1980; Morrison and Barbosa 1987). Hassell (1980), for example, studied the effects of spatial heterogeneity on a single-species system, a parasitoid-host system, and a disease-host system. Regardless of the system, he found greater population stability with more contagious distributions of animals per patch. Modeling or measuring the movement of organisms in heterogeneous landscapes (e.g., Folse et al. 1989; Crist et al. 1992; Gustafson and Gardner 1996) is another aspect of this work. Without question, spatial heterogeneity and the potential for an organism to disperse fundamentally alter species interactions and dynamics (Levin 1976). Despite the growing emphasis on spatial relationships, the supporting theory is still in its infancy (de Roos and Sabelis 1995).

Conclusions

Significant differences in the composition and structure of the study landscape were related to both physical environment and ownership. However, simple comparisons were often confounded by the interaction between ownership and physical environment on land use. For example, public land had a finer grain-size compared to private land on moraine, but the opposite was found on outwash. Comparisons of landscape pattern should be done within the context of a multifactor (climate, physiography, soil, and vegetation) ecosystem classification. Such an approach is essential for better understanding the interactions between the landscape, the physical environment, and the cultural and social forces that have shaped landscapes in the past and will shape them in the future.

Characterizing the relation between structure and function has been a central theme in many ecological studies (e.g., Watt 1947). The importance of structure, or how components are distributed in time and space, in affecting ecological processes is widely acknowledged, as is the fact that ecological processes, in turn, can create structure or pattern. Recognizing the nexus between pattern and process, along with considering the importance of scale when defining and quantifying heterogeneity, are necessary prerequisites for understanding the mechanisms that create pattern.

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References

Albert, D.A., Denton, S.R. and Barnes, B.V. 1986. Regional landscape ecosystems of Michigan. School of Natural Resources, University of Michigan. Ann Arbor, MI.

Albert, D.A. 1995. Regional landscape ecosystems of Michigan, Minnesota and Wisconsin; a working map and classification. USDA Forest Service, General Technical Report NC-178. St. Paul, MN.

Andersen, O., Crow, T.R., Lietz, S.M. and Stearns, F. 1996. Transformation of a landscape in the upper mid-west, USA: the history of the lower St. Croix river valley, 1830 to present. Landscape Urban Planning 35: 247–267.

Anderson, J.R., Hardy, E.E., Roach, J.T. and Witmer, R.E. 1976. A land use and land cover classification system for use with remote sensor data. Geological Survey Professional Paper 964. U.S. Government Printing Office, Washington.

Barnes, B.V., Zak, D.R., Denton, S.R. and Spurr, S.H. 1998. Forest Ecology, 4th Edition. John Wiley & Sons, New York.

Brouwer, F.M. 1989. Determination of broad-scale land use changes by climate and soils. J. Env. Manag. 29: 1–15.

Clayton. L. 1984. Pleistocene geology of the Superior Region, Wisconsin. University of Wisconsin Geological and Natural History Survey, Information Circular Number 46, Madison, WI.

Crist, T.O., Guertin, D.S., Wiens, J.A. and Milne, B.T. 1992. Animal movement in heterogeneous landscapes: an experiment with Eledoes beetles in shortgrass prairie. Funct. Ecol. 6: 536–544.

Curtis, J.T. 1959. The Vegetation of Wisconsin. University of Wisconsin Press, Madison, WI.

de Roos, A.M. and Sabelis, M.W. 1995. Why does space matter? In a spatial world it is hard to see the forest before the trees. Oikos 74: 347–348.

Flader, S.L. (ed.). 1983. The Great Lakes Forest, an Environmental and Social History. University of Minnesota Press, Minneapolis.

Folse, L.J., Packard, J.M. and Grant, W.E. 1989. AI modelling of animal movements in a heterogeneous habitat. Ecological Modelling 46: 57–72.

Forman, R.T.T. 1995a. Land Mosaics: the Ecology of Landscapes and Regions. Cambridge University Press, Cambridge.

Forman, R.T.T. 1995b. Some general principles of landscape and regional ecology. Landscape Ecol. 10: 133–142.

Frelich, L.E. and Graumlich, L.J. 1994. Age-class distribution and spatial patterns in an old-growth hemlock-hardwood forest. Can. J. For. Res. 24: 1939–1947.

Gustafson, E.J. and Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94–107.

Hassell, M.P. 1980. Some consequences of habitat heterogeneity for population dynamics. Oikos 35: 150–160.

Heinselman, M.L. 1973. Fire in the virgin forests of the Boundary Waters Canoe Area, Minnesota. Quat. Res. 3: 329–382.

Host, G.E., Polzer, P.L., Mladenoff, D.J. White, M.A. and Crow, T.R. 1996. A quantitative approach to developing regional ecosystem classifications. Ecol. Appl. 6: 608–618.

Keys, J.E., Jr. and Carpenter, C.A. (eds.). 1995. Ecological units of the eastern United States; first approximation. USDA Forest Service, Washington, DC.

Kotliar, N.B. and Wiens, J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos 59: 253–260.

Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V. and Coleman, P.R. 1987. Landscape patterns in a disturbed environment. Oikos 48: 321–324.

Levin, S.A. 1976. Population dynamic models in heterogeneous environments. Ann. Rev. Ecol. Syst. 7: 287–310.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73: 1943–1967.

Li, H. and Reynolds, J.F. 1994.A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75: 2446–2455.

McGarigal, K. and Marks, B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA Forest Service, Pacific Northwest Station, GTR-351. Portland, OR.

Meyer, W.B. and Turner II, B.L. (eds.). 1994. Changes in Land Use and Land Cover: A Global Perspective. Cambridge University Press, Cambridge.

Milne, B.T. 1991. Heterogeneity as a multiscale characteristic of landscapes. *In* Ecological Heterogeneity, pp. 69–84. Edited by J. Kolasa and S.T.A. Pickett. Springer-Verlag, New York.

Mladenoff, D.J., White, M.A., Pastor, J. and Crow, T.R. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecol. Appl. 3: 294–306.

Morrison, G. and Barbosa, P. 1987. Spatial heterogeneity, population 'regulation' and local extinction in simulated host-parasitoid interactions. Oecologia 73: 609–614.

Nassauer, J.I. 1995. Culture and changing landscape structure. Landscape Ecology 10: 229–237.

Nassauer, J.I. (ed.). 1997. Placing Nature: Culture and Landscape Ecology. Island Press, Washington, D.C.

Naveh, Z. 1995. Interactions of landscapes and cultures. Landscape Urban Planning 32: 43–54.

Parker, L. 1997. Restaging an evolutionary drama: thinking big on the Chequamegon and Nicolet National Forests. *In* Creating a Forestry for the 21st Century, pp. 218–219. Edited by K.A. Kohm and J.F. Franklin. Island Press, Washington, DC.

Runkle, J.R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern north America. Ecology 63: 1533–1546.

Russell, E.W.B. 1997. People and the Land Through Time: Linking Ecology and History. Yale University Press, New Haven.

SAS Institute Inc. 1988. SAS/STAT©User's Guide, Release 6.03 Edition, Cary, NC.

Turner, M.G., Wear, D.N. and Flamm, R.O. 1996. Land ownership and land-cover change in the southern Appalachian highlands and the Olympic Peninsula. Ecological Applications 6: 1150–1172.

Watt, A.S. 1947. Pattern and process in the plant community. J. Ecology 35: 1–22.

Wear, D.N. and Flamm, R.O. 1993. Public and private disturbance regimes in the Southern Appalachians. Nat. Res. Modeling 7: 379–397.

Wear, D.N., Turner, M.G. and Flamm, R.O. 1996. Ecosystem management with multiple owners: landscape dynamics in a southern Appalachian watershed. Ecol. Appl. 6: 1173–1188.

Whitney, G.G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. Ecology 67: 1548–1559.

Wiens, J.A. 1976. Population responses to patchy environments. Ann. Rev. Ecol. Syst. 7: 81–120.