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Vegetation responses to landscape structure at multiple scales across a Northern Wisconsin, USA, pine barrens landscape

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Abstract

Increasing awareness of the importance of scale and landscape structure to landscape processes and concern about loss of biodiversity has resulted in efforts to understand patterns of biodiversity across multiple scales. We examined plant species distributions and their relationships to landscape structure at varying spatial scales across a pine barrens landscape in northern Wisconsin, U.S.A. We recorded plant species cover in 1 × 1 m plots every 5 m along a 3575 m transect, along with variables describing macro- and micro-landscape structure. A total of 139 understory plant species were recorded. The distributions of many species appeared to be strongly associated with landscape structural features, such as distinct management patches and roads. TWINSPAN and detrended correspondence analysis (DCA) identified three groups of species that overlapped extensively in the ordination, possibly reflecting the relatively homogeneous nature of disturbance in the pine barrens landscape. Distribution of understory plants did not reflect all of the patch types we identified along the transect; plot ordination and classification resulted in three to five plot groups that differed in niche breadth. Wavelet transforms showed varying relationships between landscape features and plant diversity indices (Shannon–Weiner, Simpson's Dominance) at different resolutions. Wavelet variances indicated that patterns of Shannon diversity were dominated by coarse resolutions ranging from ~900–1500 m, which may have been related to topography. Patterns of Simpson's Dominance were dominated by ~700 m resolution, possibly associated with canopy cover. However, a strong correspondence between overstory patch type and diversity was found for several patch types at ranges of scales that varied by patch type. Effects of linear features such as roads were apparent in the wavelet transforms at resolutions of about 5–1000 m, suggesting roads may have an important impact on plant diversity at landscape scales. At broad scales, landscape context appeared more important to diversity than individual patches, suggesting that changes in structure at fine resolutions could alter overall diversity characteristics of the landscape. Therefore, a hierarchical perspective is necessary to recognize potential large-scale change resulting from small-scale activities.

Introduction

Understanding relationships between ecological processes and structural patterns across ecosystems is a topic of much recent and current interest among ecological researchers, theorists, and resource managers (e.g., Krummel et al. 1987; Turner 1989; Holling 1992; Levin 1992). While research in landscape ecology over the past two decades has focused primarily on structural attributes of landscapes (Golley 1995), more emphasis has been placed in recent years on understanding functional responses of organisms to spatial heterogeneity (e.g., Wiens et al. 1993). Increasing acceptance that human beings are an intrinsic part of nature has resulted in a growing interest, for both practical and theoretical purposes, in comprehending how human activities impact our biotic resources. Ultimately, additional information regarding these functional relationships should help with understanding of much-debated ecological issues such as reserve

design, resource sustainability, and conservation of biological diversity.

How responses to spatial heterogeneity change with scale of observation is likewise of critical importance for theoretical and applied work (see Allen & Starr 1982; Saunders et al. 1998), particularly since ecosystem management has become the dominant paradigm on federal lands (see Grumbine 1997; Franklin 1997). Franklin (1997) suggests that sustainability, defined as 'maintenance of the potential for... ecosystems to produce the same quality and quantity of goods in perpetuity,' is the basic premise of ecosystem management. Further, ecosystem management considers ecosystems at multiple spatial and temporal scales with recognition that management activities at one scale often have unexpected or undesirable effects at other scales (i.e., scaling effects). Understanding relationships between ecosystem processes and patterns, which ultimately control this production of goods and services, is therefore necessary for successful implementation of ecosystem management.

Loss of biological diversity due to human activities is a growing concern. Langner & Flather (1994) report considerable changes in the distribution and abundance of native species in the United States over the last 300 years, with dramatic declines in the last 30 years. Increasing fragmentation of landscapes in both temperate and tropical biomes has resulted in compositional changes in vegetation, including an increase in occurrence of exotic and disturbance-adapted species (e.g., Palik & Murphy 1990; Laurance 1991; Brothers & Spingarn 1992; DeFerrari & Naiman 1994; Matlack 1994). Traditional conservation approaches have focused on protecting high profile species. However, the species-based approach does little to protect the multitude of unknown species, some of which may be critical to maintaining functional integrity of ecosystems and landscapes (Wilson 1985; Franklin 1993).

Traditional studies of species-habitat relationships have focused on specific patches defined by ecosystem characteristics such as vegetation type, landform, and soils (e.g., Pregitzer & Barnes 1984; Lapin & Barnes 1995). These studies have provided valuable information at the plot or stand level but no direct information at landscape levels. Investigation of spatial relationships between landscape features and resources such as plant diversity improves understanding of variation in the resources throughout the landscape. Careful examination of multiple scales is necessary to ensure that plant diversity is managed at appropriate resolutions for maintenance of desired characteristics.

Successful conservation of biological diversity requires a shift toward maintaining adequate habitats and functioning ecosystems within the context of overall landscape complexity, varied objectives, and multiple spatial and temporal scales (Hansen et al. 1992; Franklin 1993). This approach requires knowledge of relationships between management activities, landscape structure, habitat use, and biological diversity at varying scales. However, empirical studies across large areas are rare because of the time, expense, and other difficulties inherent in collecting information at these scales. Remotely sensed data provide the bulk of landscape level information, but are often not detailed enough to provide accurate information at very fine resolutions.

In this project, we studied vegetation at a fine grain across a relatively broad extent to aid in developing accurate generalizations across multiple scales for this landscape. We investigated the responses of understory vascular plants to landscape structure at multiple spatial resolutions within a managed jack pine (*Pinus banksiana*) barrens landscape in northern Wisconsin. This landscape is of particular interest to managers, who are attempting to restore large tracts of land in the Chequamegon National Forest to this once-dominant ecosystem type (USDA Forest Service 1994). Our primary objectives were (1) to identify patterns of understory plant composition and diversity and describe their relationships with landscape structural attributes, and (2) to describe how the relationship between plant diversity and landscape structure changes with changing spatial resolution.

Study area

Our study area was located within the Washburn Ranger District of the Chequamegon National Forest, Wisconsin, USA, in the Bayfield Barrens subsection of the northern Minnesota section (Albert 1995). The area is characterized by Precambrian shield bedrock and late Wisconsin-age glaciated landscapes. Topography is flat to rolling, with terrace and pitted outwash landforms composed of deep, coarse-textured soils (i.e., sand, loamy sand). The climate is characterized by short, hot summers with a growing season of 120–140 days, and cold winters. Annual precipitation is 762–813 mm, and elevations range from 232–459 m (Albert 1995).

The current study was conducted in the Moquah Pine Barrens Wildlife Management Area, located in the northern portion of the Washburn Ranger District (46°37′15" N, 91°15′–91°17′ W). Though the area is primarily considered pine barrens, vegetation is sometimes more typical of savanna or brush prairie (USDA Forest Service 1994). The landscape is composed primarily of large open, often shrubby areas with scattered young jack pine and infrequent older red pine (*Pinus resinosa*, up to 200 years old). Scattered patches of regenerating or mature aspen (*Populus* spp.), oak (*Quercus* spp.), and maple (*Acer* spp.) are also part of the mosaic. Understory vegetation consists primarily of grasses, sedges, Ericaceous shrubs, sweet-fern (*Comptonia peregrina*), bracken fern (*Pteridium aquilinum*), young scrub oak (*Quercus ellipsoidalis*), young red and jack pine, and hazel (*Corylus* spp.), in varying abundances throughout the landscape.

The jack pine barrens was a dominant ecosystem type in northern Wisconsin before European settlement, occupying about 930 810 ha (Curtis 1959). The Chequamegon National Forest contained about 15 400 ha of pine barrens (USDA Forest Service 1994). However, plowing and establishment of dense pine plantations in much of the area reduced the portion of land occupied by barrens to about 3200 ha by 1990 (USDA Forest Service 1994). Managers are attempting to restore some portions of the landscape (~1133 ha) to this ecosystem type because of its prior dominance and its importance for plant and wildlife habitat (e.g., sharp-tail grouse) and recreation (e.g., berry pickers) (Vora 1993). The pine barrens landscape in the Moquah Wildlife Area is maintained using prescribed burns at intervals of 5–10 years. In restoration areas, trees are harvested and the area is then burned every 5–25 years. Over time the flora responds to the frequent fire disturbance, becoming dominated by vegetation typical of open pine barrens or savanna.

Methods

Sampling procedure

Understory vascular plants (i.e., shrubs, herbs, seedlings, and saplings) were sampled systematically in 1 × 1 m plots every five meters (as measured along the ground) along a 3575 m west-east oriented transect located in the Moquah Pine Barrens of the Chequamegon National Forest. Transect location was determined after examining aerial photos and stand maps. The transect was established so that it was located centrally within the Moquah Pine Barrens Wildlife Management Area, and it encountered as many patches 'typical' of this landscape as possible.

Sampling of most of the transect was conducted during July and August of 1994, with the last 980 m sampled in August 1995. Within each sampling plot, all understory vascular plants were identified to species when possible. Percent cover of individual species and total combined understory vegetation were estimated using a quadrat marked off into tenths on each side. In addition, canopy cover (if any) was estimated using a spherical canopy densiometer. Percentages of bare ground, woody debris, vegetative litter, and overstory tree trunks were also noted, and duff depth (cm) was measured. Additional measurements included patch type (see below), distance to edges (e.g., other patch types, roads, powerline corridors, etc.) within 80 m, aspect, slope, and microtopography characteristics.

We described the patch (i.e., ecosystem) type for each plot based on differences in vegetative structure, overstory composition, and management regime. For example, mature hardwood stands were distinguished from regenerating hardwoods; recently burned pine barrens were perceived as distinct from barrens that showed no signs of recent burning. Patches less than 25 m long (containing fewer than five sampling plots) were not analyzed as independent patches but were noted as included features in surrounding patches.

Analysis

Frequency and average percent cover of all taxa present along the transect were calculated and tabulated. Abundance of each plant species was also plotted against distance along the transect to help assess distributional patterns and possible relationships with landscape structural features, such as specific patch types or corridors. Richness (both total number of species and average number of species per plot) was calculated for each patch type (α-diversity), as well as for the entire transect (γ-diversity). Two additional diversity measures were calculated: Shannon–Weiner Diversity Index (H′) and Simpson's Dominance Index (D) (Magurran 1988).

Detrended correspondence analysis (DCA, Hill & Gauch 1980) and two-way indicator species analysis (TWINSPAN, Hill 1979) were performed on plant species, individual plots, and patch types using PC-ORD version 3.0 (McCune & Mefford 1997). Classi-

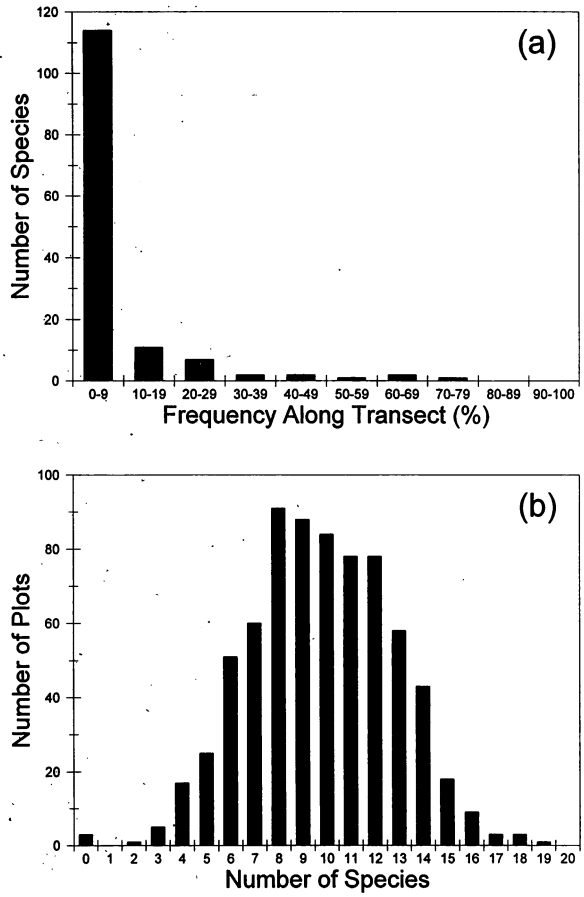

Figure 1. Frequency distribution of understory plants along a 3575 m transect running through a jack pine barrens landscape in northern Wisconsin. Most species occurred in less than 10% of the 716 plots sampled (a), and most plots contained from 4–16 species (b).

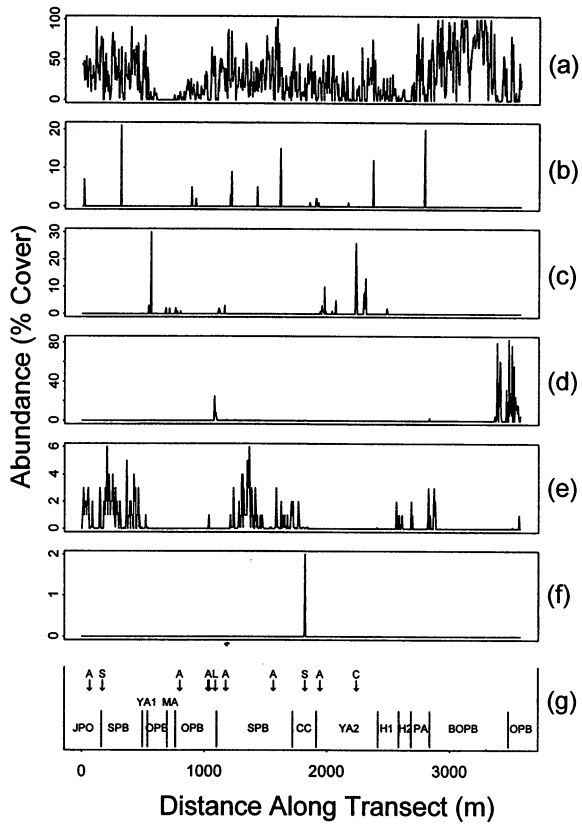

Figure 2. Relationships between distributions of six understory plant species and landscape structure along the pine barrens transect. Species shown are representative of typical distribution patterns and include: *Pteridium aquilinum* (a); *Amelanchier arborea* (b); *Hieracium aurantiacum* (c); *Conyza canadensis* (d); *Trientalis borealis* (e); and *Trifolium pratense* (f). The diagram at the bottom (g) shows landscape structure along the transect; lines correspond to edges between management or overstory patches, and arrows represent linear or small features. Refer to Table 1 for patch type codes.

fication of patch types was accomplished by averaging species abundance values by patch type; all ordinations were based on plot-level data. This analysis was done to determine whether distinct understory plant communities existed and to assess similarity between patches based on ordination of plots included in each type. Correlations were calculated between each DCA axis and the following structural and environmental variables: canopy cover (%), litter cover (%), woody debris cover (%), bare ground (%), slope (°), relative elevation (m), soil moisture (% volumetric content), average daily soil and surface temperatures (°C), and soil and surface temperatures (°C) at four times of the day (see Saunders et al. 1998, for temperature and elevation data).

To assess effects of scale on plant diversity, we used wavelet analysis to evaluate patterns of Shannon-Weiner and Simpson's measures along the transect at resolutions of 5–1500 m. Advantages of this technique include the ability to retain locational information for the transect as well as elimination of the need to assume stationarity (i.e., constant mean and variance) in the data (Bradshaw & Spies 1992). Wavelet analysis moves a window of the appropriate scale through the data, comparing the pattern in the data, $f(x)$, to that of a known analyzing wavelet, $g(x)$. This results in transformed data whose values express degree of similarity to the specified analyzing wavelet. The wavelet transform can be discretely defined as:

$$W(a,b) = \frac{1}{a}\sum f(x)^* g\left(\frac{x-b}{a}\right), \qquad (1)$$

where a represents the scale or dimension of the analyzing wavelet and b is the central point of the analysis window. We used a Mexican-hat analyzing wavelet that identifies peaks and troughs in the data; the program was developed by Li and Loehle (1995). The resulting image was used to identify understory diversity 'patches' at varying scales throughout the landscape and to determine whether those diversity patches corresponded with the overstory patch types we identified in the field. In addition, we calculated the wavelet variance, $V(a)$, as:

$$V(a) = \frac{1}{n} \sum W^2(a, b), \qquad (2)$$

where n is length of the transect, to determine whether any one scale contributed more or less than others to the overall pattern of diversity across the landscape (Bradshaw & Spies 1992).

Results

We identified 11 different patch types along our transect (Table 1). Two sandy roads with light use, six closed access roads, an old harvest landing, and a small clearing also intersected the transect. These contained from 1 to 5 sampling plots (i.e., 5–25 m). Two patch types (open pine barrens and shrubby pine barrens) occurred in more than one segment, separated by other patches. Diversity measures (Table 2) ranged from 0.90 and 6.5 (Shannon diversity and richness, respectively) in the H2 patch type, to 1.65 and 14.1 in the YA1 patch type. Lowest dominance (D) was found in YA1, while the hardwood types (H1 and H2) had the highest dominance measures. Overall dominance was relatively low (<0.50), suggesting that species cover was distributed relatively evenly.

We recorded 139 understory plant taxa in 716 plots along our transect (see Appendix 1). Four species (*Pteridium aquilinum*, *Aster macrophyllus*, *Vaccinium angustifolium*, and *Carex pensylvanica*) were very common, occurring in more than 50% of the plots. Most species, however, were relatively uncommon, occurring in fewer than 10% of the sampled plots (Figure 1a). The number of species per plot varied from zero to 19, with an average of 10 (Figure 1b).

Distributional patterns varied by species. Figure 2 shows six species representative of the different patterns. In general, the most common species tended to occur along the entire transect (e.g., Figure 2a). Many species, though relatively rare, were also found throughout the landscape (Figure 2b). However, many other species of all frequencies displayed obvious associations with specific patch types or structural features. For example, *Hieracium aurantiacum* was usually found near roads, but occasionally near other edges as well (Figure 2c). *Conyza canadensis* occurred primarily at the end of the transect, near the edge of the burned area, although its few other occurrences were also associated with edges and/or disturbed areas (Figure 2d). Distributions of some relatively common plant species, such as *Trientalis borealis* (25% frequency) were patchy, the occurrences seemingly distributed regularly throughout the landscape (Figure 2e). Finally, 17 species were very rare, found only once along the transect (Figure 2f). Because of their rarity, no conclusions could be reached regarding their associations with structural features of the landscape.

TWINSPAN results included several groupings of species (Figure 3a), but these did not appear to be distinctive when 95% confidence ellipses were drawn about the major groups in the ordination diagram (Figure 3b). The large amount of overlap suggested that no discrete compositional groups existed along the first two DCA axes. Little correlation was found between the DCA axes and the various structural and environmental variables we measured (see Methods). Weak correlations were found between Axis 1 and (a) percent canopy cover ($R = -0.45$); and (b) elevation ($R = 0.31$). No relationships with measured variables were found to explain the variation along Axis 2.

TWINSPAN classification of patch types produced five groupings (Figure 4a) with varying environmental niches along the first two ordination axes (Figures 4b–f). The TWINSPAN groupings appeared generally consistent with the individual ordinations. For example, Group 5 (Figure 4f) included three patch types whose ordinations were all constrained along Axis 2. The YA2 patch type (Figure 4b) seemed unique, with Axis 1 scores similar to Group 5, but with more variation along Axis 2. Two patch types in Group 4 (Figure 4e) appeared somewhat constrained by Axis 2 and therefore might be more appropriately linked with Group 5. This possible misclassification could be due to the small number of plots contained within each of these patch types (see Table 1). Further, Groups 2-4 (Figures 4c–e) did not appear to be significantly different, since they all had similar variation and centroid locations. Therefore, stopping at the second branching of the TWINSPAN diagram when forming groups might be sufficient. Total variation may have been so small that the divisions were not ecologically distinc-

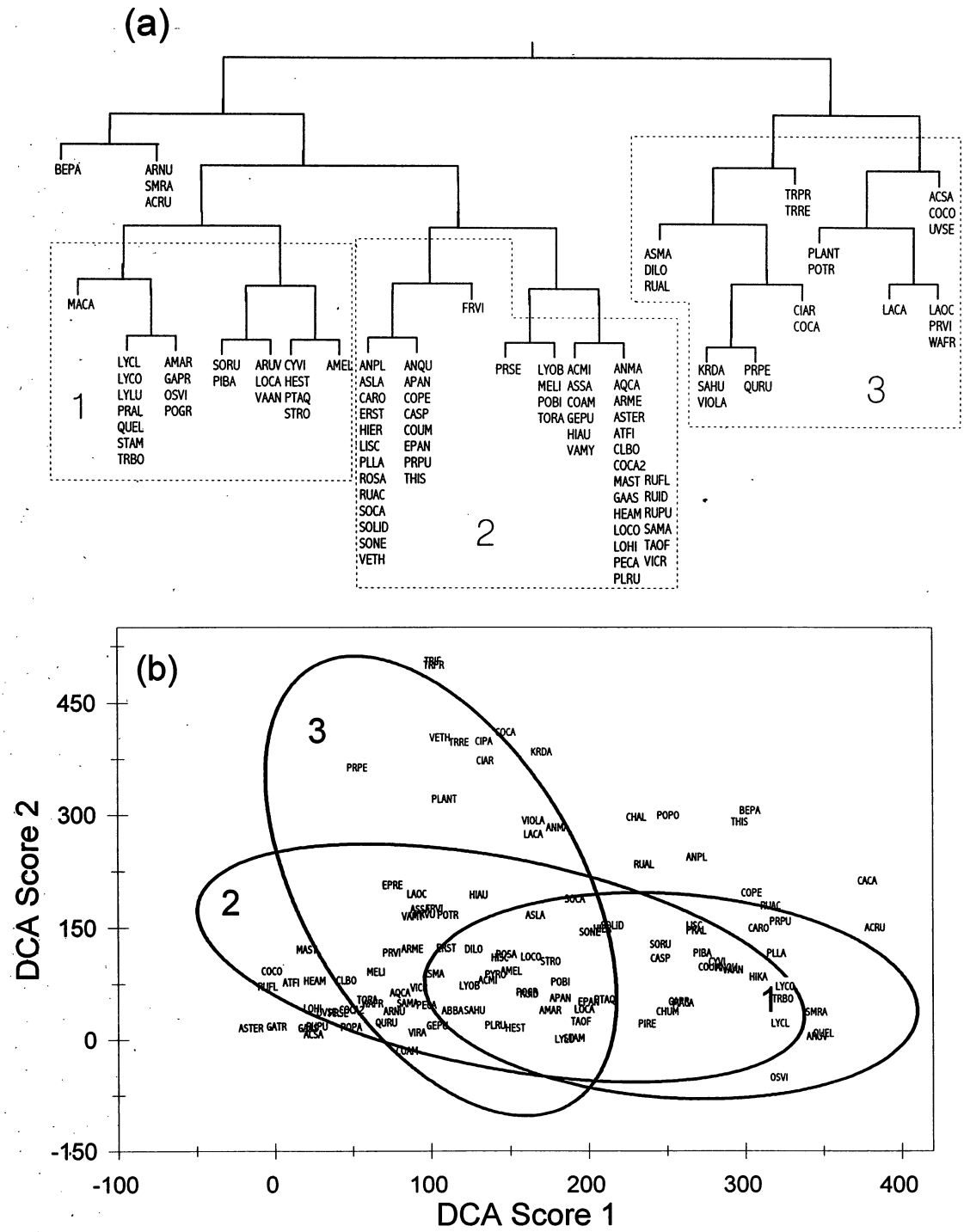

Figure 3. TWINSPAN classification (a) and DCA ordination (b) of plant species occurring along the pine barrens transect. The three large groups identified in the classification correspond to the 95% confidence ellipses in the ordination. Eigenvalues are 0.517 for Axis 1 and 0.406 for Axis 2. See Appendix for species codes.

Table 1. Characteristics and locations of patch types along the pine barrens (PB) transect in Chequamegon National Forest, WI. Patch types were delineated based on perceived differences in community structure and composition. A total of 716 plots were sampled, with number of plots occurring in each patch type indicated below. Height, age, and diameter at breast height (DBH) data are based on trees sampled within a 10 m radius circular plot.

Patch Type Code	Description	Start (m)	End (m)[a]	No. plots	Avg. canopy cover (%)	No. unique species	Total no. species
JPO	jack pine and pin oak stand, originated 1940, burned 1994; height ~10 m; *Quercus ellipsoidalis* mean dbh = 11.5 cm ($n = 26$)	0	160	33	88	0	33
SPB	shrubby pine barrens: dense upland brush (e.g., *Corylus, Quercus, Populus*)	175 1065	495 1720	199	0	5	80
YA1	young aspen: dense *Populus tremuloides*, age<10 years, height 3–4 m.	500	535	8	46	1	37
OPB	open pine barrens: *Comptonia peregrina* and *Vaccinium* spp. groundlayer; scattered red and jack pine	540 770 3490	695 1060 3575	110	2	2	70
MA	mature aspen: *Populus tremuloides*, age ~47 years, height ~16 m; mean dbh = 12.9 cm ($n = 23$)	700	765	14	49	0	33
CC	clearcut (cut 1989); shrubby, w/ considerable logging slash	1725	1915	39	0	6	61
YA2	young aspen: *P. tremuloides*, age = 22 years, height ~8 m, mean dbh = 8.2 cm ($n = 76$)	1920	2415	100	89	9	79
H1	hardwoods: mature aspen, maple, oak; dense *Corylus* brush	2420	2585	34	98	1	39
H2	hardwoods: oak and maple, open understory; age = 62 years, height ~16 m; *Quercus rubra* mean dbh = 16.6 cm ($n = 25$); *Acer* spp. mean dbh = 8.5 cm ($n = 24$)	2590	2685	20	100	2	29
PA	mixed jack, red, and white pine, aspen; dense shrub layer, primarily *Corylus*; height ~14 m; *Pinus* spp. mean dbh = 25.5 cm ($n = 5$); *Populus* spp. mean dbh = 26.8 cm ($n = 3$)	2690	2835	30	90	2	47
BOPB	recently burned area (1994) on open pine barrens	2840	3480	129	2	1	61

[a]Old access roads (code 'A') occur at meters 65, 800, 1030, 1040, 1175, and 1940–1955; sand roads (light use, code 'S') at meters 165–170 and 1820; an old harvest landing (code 'L') at meters 1080–1100; and a small clearing (code 'C') at meters 2235–2240.

tive. Finally, the JPO (Figure 4c) patch type had very small variation along both axes and was completely contained within the ellipse for the SPB patch type. This suggests that JPO may have been more limited in niche breadth than SPB but was not significantly different from it.

The wavelet transform images suggested a close relationship between landscape structure (as defined by patches, edges, and corridors) and measures of plant diversity at varying resolutions (Figure 5). For example, the open pine barrens (OPB) in the first half of the transect corresponded with lighter areas (i.e., lower diversity), while the shrubby pine barrens (SPB) was associated with primarily darker shading (i.e., higher diversity) in the transform (Figure 5a). (Note: The lighter area that appeared in SPB at ~1500–1700 m seemed to be related to an included corridor; see below). However, the first lower diversity 'patch' associated with OPB was less distinct and occurred at a finer resolution (~250–500 m) than the second (~300–1000 m). The edge between YA2 and H1 was less distinct than that between OPB and SPB, especially at coarser resolutions (e.g., 800-1200 m). Some patches seemed to function as ecotones between 'patches' of high and low diversity. Two of these were CC and PA, which displayed image shadings intermediate between the patches on either side. Other patches, such as H1, were associated with intermediate to high diversities at certain scales (i.e., darker shading to ~500 m) but were associated with relatively low diversity at coarser resolutions (i.e., >500 m).

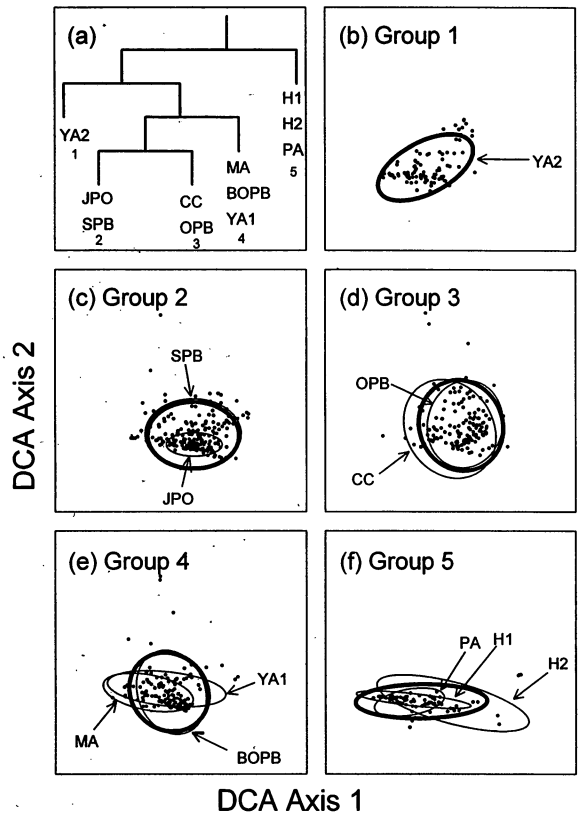

Figure 4. TWINSPAN classification of patch types (a) and DCA ordination of sampling plots (b–f) along the pine barrens transect. In (b) through (f), lighter lines represent 95% confidence ellipses for individual patch types (labelled) and heavy lines represent 95% confidence ellipses for all patch types combined within each group (all plots are on the same scale). Groups are based on the TWINSPAN classification. See Table 1 for patch type codes.

Table 2. Values of diversity indices averaged over each patch type. Values are means (one standard error) for each patch type and the entire transect (716 plots).

Patch Type	Shannon–Weiner (H′)	Simpson's dominance (D)	Richness
JPO	1.16 (0.08)	0.43 (0.03)	8.1 (0.38)
SPB	1.29 (0.03)	0.38 (0.01)	10.2 (0.21)
YA1	1.65 (0.09)	0.28 (0.04)	14.1 (0.74)
OPB	1.14 (0.03)	0.41 (0.02)	9.1 (0.25)
MA	1.39 (0.08)	0.34 (0.03)	11.6 (0.77)
CC	1.33 (0.06)	0.35 (0.03)	10.4 (0.40)
YA2	1.37 (0.04)	0.34 (0.02)	11.3 (0.28)
H1	1.04 (0.06)	0.50 (0.06)	8.5 (0.42)
H2	0.90 (0.11)	0.49 (0.07)	6.5 (0.67)
PA	1.37 (0.07)	0.35 (0.03)	10.5 (0.45)
BOPB	1.15 (0.04)	0.43 (0.02)	8.9 (0.24)
overall	1.24 (0.02)	0.39 (0.01)	9.8 (0.11)

Roads also had an apparent effect on diversity. The access road and/or MA (mature aspen) patch edge near meter 800 was related to a high diversity patch up to about 500-m resolution. The road near meter 1600 was centered on an area of low diversity that was apparent at a wide range of resolutions. Furthermore, this area of low diversity appeared to extend much farther (200–300 m) than might have been expected given the width (~5 m) and level of use of the road (closed road, no official use). Interestingly, the forest road near meter 1800, though it received some use (unlike the access roads), showed an association with only a small, indistinct diversity 'patch' at fine resolutions (<200 m).

The wavelet transform for Simpson's dominance (Figure 5b) appeared to produce a reverse image of the transform for Shannon diversity (i.e., the same 'patches' exist, but what is dark in the Shannon image is light in Simpson's). Again, darker shading indicates higher index values, or greater dominance in this case. Where there was high diversity, dominance was low; or conversely, evenness was high. Landscape structure associations were similar to Shannon diversity, but of opposite direction. Additionally, Simpson's transform values appeared less variable than Shannon values, with less marked contrast between image 'patches'.

Not all wavelet transform 'patches' corresponded with distinct landscape features, and the converse was also true. For example, the lighter Shannon diversity patch (<500-m resolution) near the end of the transect was not associated with any landscape feature recorded in the field. Additionally, CC did not correspond with any distinct diversity 'patch' in the wavelet images.

The Shannon wavelet variance (Figure 5a, inset) increased with increasing scale until about the 900 m resolution, then remained relatively stable to the highest resolution analyzed (1500 m). This indicated that relatively coarse scales dominated the diversity pattern. The wavelet variance for Simpson's Dominance (Figure 5b, inset) showed a single peak at about the 700 m scale.

Discussion

The processes that determine distribution and diversity of plant species in a landscape (e.g., dispersal ability, competition, and environmental conditions, such as light availability (Song et al. 1997), temperature (Ross 1958), and soil characteristics (e.g., soil

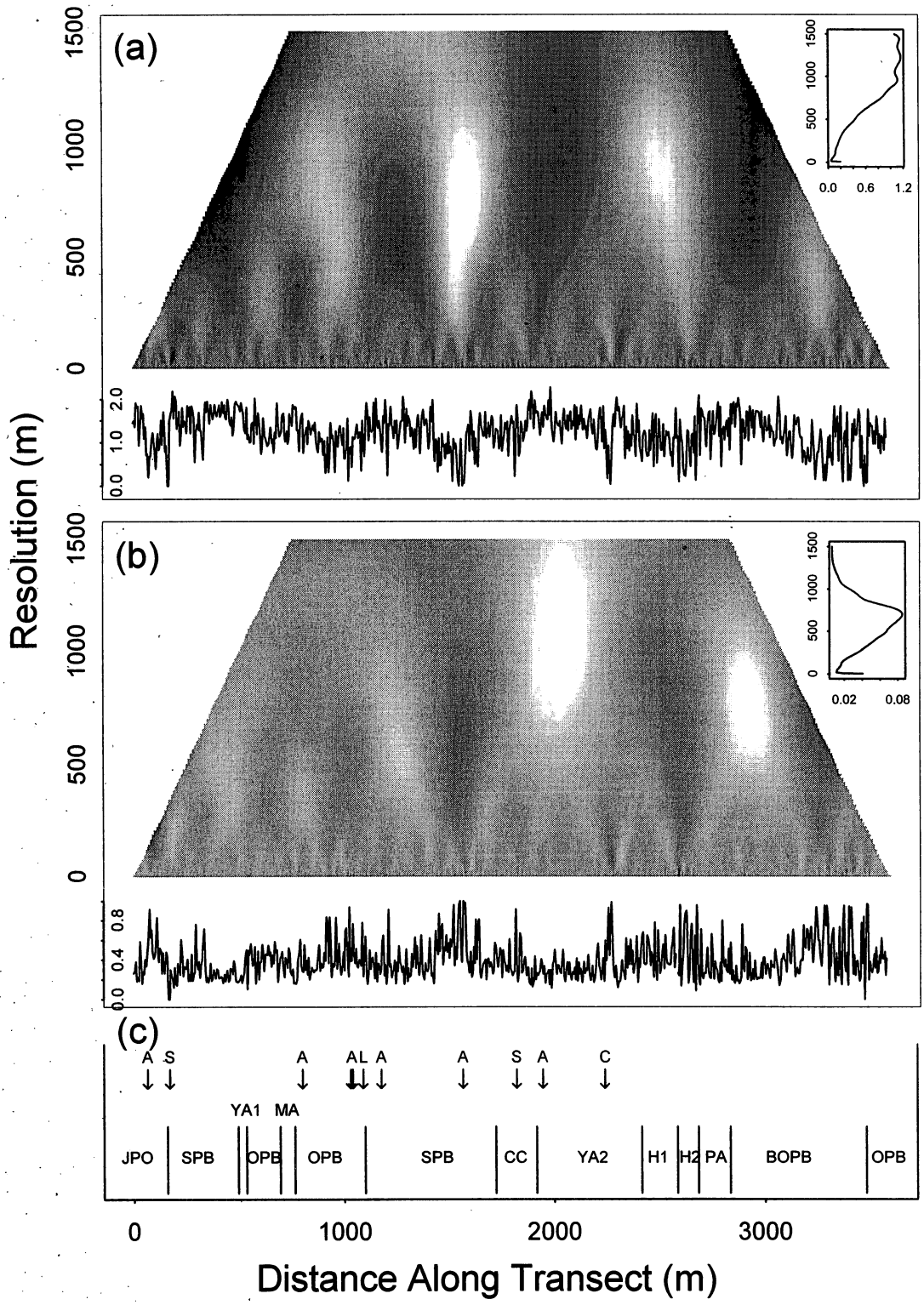

Figure 5. Relationships between understory plant diversity and landscape structure at multiple resolutions along the pine barrens transect. Shown are wavelet transforms for Shannon-Weiner Diversity (a) and Simpson's Dominance (b). The lines at the bottoms of (a) and (b) are the raw data values, and the insets are the wavelet variances. Darker areas in the wavelet images represent 'patches' of higher diversity or dominance in the landscape. The diagram at the bottom (c) shows landscape structure along the transect; lines correspond to edges between management or overstory patches, and arrows represent linear or small features. Refer to Table 1 for patch type codes.

temperature, moisture, and nutrients)) can be influenced by landscape structure. Management activities (e.g., harvesting, planting, burning) influence overstory structure and dynamics (Esseen 1994; Dale et al. 1995), creating patches and edges that can alter the microclimate (and thus possibly affect dispersal, competition, and soil processes) in and around the managed area (Chen et al. 1993). Therefore, these management practices can also influence understory species distribution.

Our first major objective was to determine whether and what kinds of relationships existed between plant distribution and landscape structure in the pine barrens landscape. While some species appeared to be randomly distributed across the landscape, others demonstrated apparent correspondence with landscape structural features such as patch type, edges, and roads. This suggested that plant species were responding to the environment in an individualistic manner.

Our classification results identified several groups of species, but the ordinations showed much overlap between the major groupings, suggesting the groups had similar environmental needs. Frequent fire disturbance is an intrinsic characteristic of the pine barrens landscape. It is necessary for continued existence of this ecosystem type. Although disturbance intensity and time since the last disturbance may vary somewhat, the pine barrens landscape is relatively homogeneous in regard to type of disturbance (i.e., fire; see USDA 1994). Therefore, environmental characteristics of patches may not have differed enough to separate plant groups more widely. Indeed, correlations indicated very weak or no relationships ($r < 0.22$) between plant ordinations and variables such as litter, woody debris, soil moisture, and surface and soil temperatures. Canopy cover did have a weak negative correlation ($r = -0.45$) with the first ordination axis, indicating that plots and species with lower Axis 1 scores occurred in areas with greater shading.

Patches and corridors are the major structural features creating heterogeneity in a landscape (Forman & Godron 1981), and we define them in this paper from a human perspective, based on management activities, composition, and height of the vegetation. Understanding the importance (i.e., weighting) of different patch types for various management objectives is crucial for successful landscape management (Crow & Gustafson 1997). The rarity of species in a landscape might prove to be a critical consideration for management of biological diversity, such as in reserve design (Noss & Cooperrider 1994).

Understory plants may not respond to the same delineation of patches perceptible from a human standpoint. They may manifest fewer or greater numbers of patches, based on their distribution and diversity. Patch classification and plot ordination indicated that some areas identified as separate patch types in the field may not have been functionally different for understory plants (also see Chen et al. 1996). Our data, for instance, suggested that plants might have only responded to three patch types (see Figure 4) instead of the eleven we initially delineated. It appeared that some patch types created more constrained niches, as suggested by limited variation along one or both of the ordination axes. Although we found little correlation between the ordination axes and the structural and environmental variables we measured, it is possible that something we did not measure directly, such as variations in disturbance characteristics, may have constrained the ordination. This may have implications for rare species. For example, Figure 4d suggested that the JPO patch type did not contribute anything different to the landscape than did SPB, but SPB might have contained some rare species that JPO did not. In fact, SPB provided 41 species that JPO did not, and JPO did not contribute any species not found in SPB. At first glance this may seem to be an artifact of area, since SPB contained a greater number of sampling plots. However, when the number of sampling plots used to calculate the SPB ellipse was randomly reduced to equal the number of plots in JPO, the result was an ellipse of about the same size as the one obtained using all the plots. This suggested that the variation might have been due to a wider range of growing conditions within a specified area.

Similarly, YA2 and the mature hardwood types (H1, H2, and PA) seemed to provide a distinct range of conditions for plants in this landscape. In fact, YA2 contained nine unique species, more than any other patch type or patch type group, perhaps explaining its separation in the classification. The hardwoods group contained seven unique species. Although the remaining groups contained from 2 to 8 unique species, their similar ordinations suggested that these species could have occurred in any of those groups.

The preceding discussion of the similarity between patch types might suggest to a resource manager that some types (i.e., JPO) are unnecessary for maintenance of understory plant diversity in this landscape or can be interchanged with other types. However, other variables, such as patch configuration, shape, size, and dispersion, will have an impact on components

of species diversity such as composition, evenness, and richness. Further study of this landscape, especially with a two-dimensional perspective, would be needed before conclusions regarding redundancy of patch types could be made.

To summarize thus far, clear relationships appeared to exist between individual species and landscape structure. However, these relationships could have been probabilistic due to a lack of direct species-habitat relationships associated with effects on patches of the surrounding matrix (i.e., landscape mosaic), or other factors such as disturbance. The current approach to preserving species by protecting individual habitat patches or ecosystems needs to be carefully reviewed, and species- and landscape-level information incorporated (Franklin 1993; Orians 1993; Naiman et al. 1993; Irwin & Wigley 1993; Wilcove 1993).

Our second primary objective was to examine how the relationship between understory plant diversity and landscape structure changed across multiple resolutions. Successful implementation of ecosystem management demands that managers move away from single-stand manipulation and begin to manage the landscape as a whole, taking into account interactions between landscape elements as well as the characteristics of individual features.

The wavelet variances suggested that the most appropriate scale for study of plant diversity in this landscape depended on the diversity index under examination. The wavelet variance for Shannon diversity suggested that diversity pattern was dominated by a wide range of coarse scales (~900–1500 m resolutions). Patterns in topographic variables (i.e., elevation) were suggestive of patterns in diversity, indicating a possible relationship between elevation and diversity at coarse scales. The single narrow peak in the Simpson's wavelet variance, however, suggested a single scale of pattern in this index at about the 700 m scale. Canopy cover patterns also appeared to be dominated by the 700 m scale, suggesting that canopy cover might be a useful variable for predicting plant dominance in this landscape. Management activities that affect structure of the overstory might act to determine dominance of plants in the landscape, although individual patch types might not influence dominance greatly.

The Shannon wavelet transform showed varying relationships between landscape features and plant diversity at different resolutions. At finer resolutions, diversity was quite variable. At these scales (i.e., stand-level or within-stand), it has been found that most understory plants are related to the heterogeneous canopy (Song et al. 1997) or to microhabitat characteristics (Whitney 1991); therefore, diversity would be expected to be more variable. At intermediate scales, diversity appeared to be related largely to individual landscape features (i.e., patches, roads). Diversity at the landscape level did not appear to correspond as much with individual landscape features as with their context within the landscape. As scale increased, diversity values prevalent in a majority of the plots (or patches) contained within the analysis window appeared to determine diversity at the next level. This provides evidence for a critical level of change at even the finest resolutions, beyond which characteristics of the entire landscape could be altered (i.e., cumulative effects). Managers should consider this when converting one patch type to another, as it may not be adequate to replace one patch with another in a different location when striving to maintain or restore overall characteristics of the landscape matrix (e.g., pine barrens). A landscape perspective is necessary to recognize potential large-scale change resulting from small-scale activities.

Roads and edges can significantly alter landscape characteristics. Our data showed apparent differential effects of roads on plant diversity among many scales. Interestingly, the roads that were not closed seemed to have little noticeable effect on diversity, but at least one of the old access roads appeared to have some influence. Although we found some evidence of roads corresponding with higher diversity, one access road was associated with very low diversity at a wide range of scales. These results suggested that the effects of roads might be somewhat unpredictable or largely dependent on surroundings (i.e., matrix) or frequency and intensity of use. For example, the road near meter 1600 was farther from edges between adjacent patches than the others and, as mentioned, seemed to be associated with a very distinct low diversity area. It has been shown that species diversity increases (and composition changes) near closed-open canopy edges (Brothers & Spingarn 1992; Fraver 1994; Matlack 1994). Perhaps effects from other types of edges masked the effects of roads on plant diversity where they were closely associated. Roads have been found to affect composition up to 200 m away (Angold 1997) and to decrease plant species richness up to 1 km away (Findlay & Houlahan 1997), although the data are few. These studies (Angold 1997; Findlay & Houlahan 1997) only examined paved roads, but our results suggest that unpaved and temporary roads also influence

plant diversity. Therefore, landscape-level interactions and features other than distinct management patches (i.e., forest stands, open areas), should be given more consideration when making management decisions.

Plant diversity at fine resolutions can be greater than that at coarse resolutions. In a similar study, Glenn-Lewin and Ver Hoef (1988) suggested that diversity at any scale was related to patch structure at that scale. Our results have largely supported this conclusion, but have also indicated that some small features that create heterogeneity in a landscape (e.g., roads) might act to decrease species diversity through homogenization of structure at broader scales (e.g., the entire landscape exists as edge habitat). This scenario might also result in high diversity of weedy or exotic species which often are better colonizers or competitors on disturbed ground, but low diversity of native species or those that require less disturbed or interior habitat.

We have found that plant species composition and diversity are at least somewhat related to the patch structure created and managed by humans in this landscape. When humans alter landscape structure, they directly influence understory vegetation as well (Abrams & Dickmann 1982; Gove et al. 1992; North et al. 1996). Therefore, it is critical to focus in future research on understanding the available alternatives for creating landscape patterns (Crow & Gustafson 1997) and their consequences for plant species composition and diversity, in order to sustain biological diversity in the face of increasing human demands on our landscapes.

We have not been concerned in this paper with examining temporal changes in diversity. Managers also have the ability to manipulate successional states through harvesting or burning. Our concern here has been to provide information on multiple-scale relationships as they currently exist between landscape structure and plant diversity in the pine barrens landscape. With this information and knowledge gained from our future and concurrent work concerning plant diversity, social and economic values, and wildlife habitat quality in this and other landscapes, we hope to build hierarchical models to provide useful information on how alternative management scenarios might affect landscape values. We feel that a hierarchical perspective is crucial to predicting effects of land management on biotic resources, and to therefore succeed in the goal of sustaining biodiversity.

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Appendix 1. Frequency and cover of understory plant species found along a 3575 m transect through a pine barrens landscape in northern Wisconsin (in order of decreasing frequency). Codes are those referred to in Figure 3. Frequency values include number (n) and percentage of plots in which a species occurred (N = 716 total plots). Cover values are average, minimum, maximum, and standard error of species percent cover along the transect. Nomenclature follows that of Gleason and Cronquist (1991).

Species	Code	Frequency		Cover (%)			
		n	%	avg	min	max	se
Herb, shrub ans tree species:							
Pteridium aquilinum	PTAQ	557	77.8	33.4	1.0	100.0	1.1
Aster macrophyllus	ASMA	477	66.6	18.7	0.1	95.0	0.9
Vaccinium angustifolium	VAAN	448	62.6	6.7	0.1	70.0	0.4
Rubus alleghaniensis	RUAL	312	43.6	12.9	0.1	90.0	1.0
Fragaria virginiana	FRVI	258	36.0	7.7	0.1	87.0	0.9
Gaultheria procumbens	GAPR	243	33.9	1.6	0.1	10.0	0.1
Maianthemum canadense	MACA	204	28.5	1.3	0.1	10.0	0.1
Corylus cornuta	COCO	193	27.0	32.4	0.1	100.0	2.0
Quercus ellipsoidalis	QUEL	192	26.8	21.3	0.1	100.0	2.1
Acer rubrum	ACRU	189	26.4	21.6	0.1	100.0	2.2
Trientalis borealis	TRBO	179	25.0	1.2	0.1	6.0	0.1
Comptonia peregrina	COPE	159	22.2	13.3	0.1	95.0	1.6
Waldsteinia fragarioides	WAFR	133	18.6	12.6	0.1	95.0	1.7
Calystegia spithamaea	CASP	121	16.9	2.3	0.1	26.0	0.3
Diervilla lonicera	DILO	120	16.8	3.3	0.1	20.0	0.3
Populus tremuloides	POTR	101	14.1	18.2	0.1	100.0	2.3
Betula papyrifera	BEPA	95	13.3	7.8	0.1	100.0	1.6
Polygonatum biflorum	POBI	87	12.2	2.7	0.1	20.0	0.4
Aster sagittifolius	ASSA	84	11.7	1.9	0.1	25.0	0.3
Lathyrus ochroleucus	LAOC	79	11.0	1.2	0.1	8.0	0.2
Viola spp.	VIOLA	78	10.9	0.6	0.1	3.0	0.1
Salix humilis	SAHU	76	10.6	21.3	0.1	100.0	3.5
Amelanchier spp.	AMEL	71	9.9	10.3	0.1	100.0	1.9
Populus grandidentata	POGR	66	9.2	15.0	0.1	87.0	2.2
Apocynum androsaemifolium	APAN	57	8.0	1.6	0.1	16.0	0.3
Prunus serotina	PRSE	52	7.3	15.1	0.1	60.0	2.2
Aralia nudicaulis	ARNU	48	6.7	3.8	0.1	22.0	0.7
Uvularia sessilifolia	UVSE	46	6.4	1.8	0.1	14.0	0.4
Prunus pumila	PRPU	42	5.9	7.0	0.1	55.0	1.7
Comandra umbellata	COUM	40	5.6	1.2	0.1	5.0	0.2
Aster laevis	ASLA	39	5.4	3.9	0.1	44.0	1.2
Conyza canadensis	COCA	38	5.3	18.7	0.1	83.0	4.0
Hieracium aurantiacum	HIAU	36	5.0	4.2	0.1	30.0	1.2
Corylus americana	COAM	32	4.5	34.9	0.1	100.0	5.4
Lycopodium obscurum	LYOB	32	4.5	1.4	0.1	4.0	0.2
Pedicularis canadensis	PECA	30	4.2	2.1	0.1	7.0	0.4
Acer saccharum	ACSA	29	4.1	13.7	0.1	80.0	4.3
Pinus banksiana	PIBA	26	3.6	5.7	0.1	26.0	1.4
Rosa spp.	ROSA	26	3.6	1.9	0.1	7.0	0.3
Streptopus roseus	STRO	25	3.5	2.4	0.1	9.0	0.5
Lactuca canadensis	LACA	24	3.4	1.2	0.1	4.0	0.3
Hieracium spp.	HIER	23	3.2	19.9	0.1	70.0	5.0
Prunus virginiana	PRVI	23	3.2	11.2	0.1	75.0	4.0
Prunus pensylvanica	PRPE	22	3.1	5.2	0.1	24.0	1.4

Appendix 1. Continued.

Species	Code	Frequency		Cover (%)			
		n	%	avg	min	max	se
Solidago spp.	SOLID	21	2.9	1.2	0.1	4.0	0.2
Vaccinium myrtilloides	VAMY	20	2.8	3.9	0.1	17.0	0.9
Aquilegia canadensis	AQCA	19	2.7	1.3	0.1	4.0	0.3
Geranium pusillum	GEPU	17	2.4	6.3	0.1	55.0	3.2
Smilacina racemosa	SMRA	17	2.4	1.6	0.1	4.0	0.3
Amelanchier arborea	AMAR	16	2.2	6.6	0.1	21.0	1.7
Anemone quinquifolia	ANQU	15	2.1	0.6	0.1	2.0	0.2
Solidago nemoralis	SONE	15	2.1	2.0	0.1	9.0	0.6
Vicia cracca	VICR	14	2.0	0.7	0.1	2.0	0.2
Lonicera hirsuta	LOHI	13	1.8	2.7	0.1	12.0	0.9
Clintonia borealis	CLBO	11	1.5	2.8	1.0	5.0	0.5
Lycopodium clavatum	LYCL	11	1.5	6.1	0.1	15.0	1.7
Rubus pubescens	RUPU	11	1.5	2.1	1.0	3.0	0.3
Solidago canadensis	SOCA	11	1.5	6.2	0.1	20.0	2.0
Erigeron strigosus	ERST	9	1.3	0.9	0.1	4.0	0.4
Sanicula marilandica	SAMA	9	1.3	2.1	0.1	9.0	0.9
Achillea millefolium	ACMI	8	1.1	11.4	0.1	75.0	9.1
Krigia dandelion	KRDA	8	1.1	0.7	0.1	2.0	0.2
Melampyrem lineare	MELI	8	1.1	0.7	0.1	2.0	0.2
Verbascum thapsus	VETH	8	1.1	2.8	0.1	18.0	2.2
Cornus canadensis	COCA2	7	1.0	2.3	0.1	9.0	1.2
Epilobium angustifolium	EPAN	7	1.0	4.1	1.0	13.0	1.7
Quercus rubra	QURU	7	1.0	2.3	0.1	6.0	0.8
Campanula rotundifolia	CARO	6	0.8	0.1	0.1	0.1	0.0
Rumex acetosella	RUAC	5	0.7	10.2	0.1	40.0	7.6
Unidentified thistle	THIS	5	0.7	2.9	0.1	14.0	2.8
Antennaria plantaginifolia	ANPL	4	0.6	1.1	0.1	3.0	0.7
Athyrium filix-femina	ATFI	4	0.6	23.0	12.0	30.0	3.9
Cirsium arvense	CIAR	4	0.6	5.8	1.0	18.0	4.1
Galium asprellum	GAAS	4	0.6	0.8	0.1	2.0	0.5
Lonicera canadensis	LOCA	4	0.6	1.5	0.1	4.0	0.9
Prenanthes alba	PRAL	4	0.6	0.8	0.1	2.0	0.5
Rubus flagellaris	RUFL	4	0.6	1.6	0.1	4.0	0.9
Rubus idaeus	RUID	4	0.6	8.1	0.1	20.0	4.9
Taraxacum officinale	TAOF	4	0.6	0.6	0.1	1.0	0.3
Anaphalis margaritacea	ANMA	3	0.4	2.7	0.1	5.0	1.4
Arctostaphylos uva-ursi	ARUV	3	0.4	4.7	1.0	8.0	2.0
Helianthus strumosus	HEST	3	0.4	3.7	1.0	9.0	2.7
Hepatica americana	HEAM	3	0.4	1.0	0.1	2.0	0.5
Lotus corniculatus	LOCO	3	0.4	15.7	2.0	25.0	7.0
Plantago rugelii	PLRU	3	0.4	0.7	0.1	2.0	0.6
Plantago spp.	PLANT	3	0.4	1.1	0.1	3.0	1.0
Solidago rugosa	SORU	3	0.4	0.7	0.1	1.0	0.3
Toxicodendron radicans	TORA	3	0.4	1.7	1.0	2.0	0.3
Chimaphila umbellata	CHUM	2	0.3	0.1	0.1	0.1	
Cynoglossum virginianum	CYVI	2	0.3	3.0	2.0	4.0	1.0
Galium triflorum	GATR	2	0.3	0.1	0.1	0.1	
Liatris scariosa var. *novae-angliae*	LISC	2	0.3	2.0	2.0	2.0	
Lycopodium complanatum	LYCO	2	0.3	1.1	0.1	2.0	1.0
Matteuccia struthiopteris	MAST	2	0.3	37.5	25.0	50.0	12.5
Ostrya virginiana	OSVI	2	0.3	9.5	7.0	12.0	2.5

Appendix 1. Continued.

Species	Code	Frequency		Cover (%)			
		n	%	avg	min	max	se
Plantago lanceolata	PLLA	2	0.3	1.1	0.1	2.0	1.0
Polygala paucifolia	POPA	2	0.3	0.6	0.1	1.0	0.5
Polygala polygama	POPO	2	0.3	0.6	0.1	1.0	0.5
Streptopus amplexifolius	STAM	2	0.3	3.5	3.0	4.0	0.5
Trifolium pratense	TRPR	2	0.3	1.1	0.1	2.0	1.0
Trifolium repens	TRRE	2	0.3	27.5	5.0	50.0	22.5
Abies balsamea	ABBA	1	0.1	0.1	0.1	0.1	
Aronia melanocarpa	ARME	1	0.1	7.0	7.0	7.0	
Aster spp.	ASTER	1	0.1		5.0	5.0	5.0
Carpinus caroliniana	CACA	1	0.1	0.1	0.1	0.1	
Chenopodium album	CHAL	1	0.1	3.0	3.0	3.0	
Cirsium palustre	CIPA	1	0.1	4.0	4.0	4.0	
Epigaea repens	EPRE	1	0.1	1.0	1.0	1.0	
Hieracium kalmii	HIKA	1	0.1	0.1	0.1	0.1	
Hieracium scabrum	HISC	1	0.1	0.1	0.1	0.1	
Lycopodium lucidulum	LYLU	1	0.1	6.0	6.0	6.0	
Pinus resinosa	PIRE	1	0.1	1.0	1.0	1.0	
Prunella vulgaris	PRVU	1	0.1	0.1	0.1	0.1	
Pyrola rotundifolia var. americana	PYRO	1	0.1	0.1	0.1	0.1	
Trifolium spp.	TRIF	1	0.1	0.1	0.1	0.1	
Viburnum rafinesquianum	VIRA	1	0.1	0.1	0.1	0.1	
Grasses, sedges, and rushes:							
Carex pensylvanica	CAPE2	389	54.3				
Oryzopsis asperifolia	ORAS	348	48.6				
Danthonia spicata	DASP	208	29.1				
Panicum depauperatum	PADE	139	19.4				
Panicum xanthophysum	PAXA	56	7.8				
Panicum lanuginosum var. *implicatum*	PALA	51	7.1				
Unidentified grass	UKGR	27	3.8				
Oryzopsis pungens	ORPU	18	2.5				
Agrostis hyemalis	AGHY	13	1.8				
Bromus ciliatus	BRCI	10	1.4				
Carex spp.	CAREX	9	1.3				
Schizachyrium scoparium	SCSC	7	1.0				
Brachyelytrum erectum	BRER	7	1.0				
Carex pedunculata	CAPE	7	1.0				
Juncus spp.	JUNC	7	1.0				
Andropogon gerardii	ANGE	2	0.3				
Bromus kalmii	BRKA	2	0.3				
Elytrigia repens	ELRE	2	0.3				
Festuca ovina	FEOV	2	0.3				
Koeleria pyramidata	KOPY	2	0.3				
Muhlenbergia mexicana	MUME	1	0.1				
Schizachne purpurascens	SCPU	1	0.1				