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The patch mosaic and ecological decomposition across spatial scales in a managed landscape of northern Wisconsin, USA

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Abstract

Understanding landscape organization across scales is vital for determining the impacts of management and retaining structurally and functionally diverse ecosystems. We studied the relationships of a functional variable, decomposition, to microclimatic, vegetative and structural features at multiple scales in two distinct landscapes of northern Wisconsin, USA. We hoped to elucidate any characteristic resolutions of structure-process relationships on these landscapes, and to determine the validity of extrapolation of structure-process associations across scales and management regimes. We used a combination of ANOVA, wavelet, canonical discriminant, and correlation analyses and asked specifically whether: 1) specific combinations of microclimatic, structural, and vegetative features were consistently associated with differences in decomposition among management zones along transects (i.e., within landscapes); and 2) factors influencing decomposition were consistent among resolutions of analysis and depths within and between landscapes. Decomposition was greater on the pine barrens than the small block transect and greater at 4 cm depth than at the surface for both landscapes. Significant differences in decomposition occurred among management patches for both transects and depths, except 4 cm along the pine barrens. In general decomposition was faster for patch types with greater overstory cover at 1 cm (both transects) and lower at 4 cm (small block). Canonical discriminant analysis also separated management patches by overstory cover for both transects. Secondary vectors also separated patches along both transects by microclimate, independent from overstory effects on those variables. Dominant resolutions in the patterns of decomposition differed between transects and depths: 80 m (pine barrens, 1 cm); 500 m (pine barrens 4 cm); 160 m (small block, 1 cm); and 750 m (small block, 4 cm). At the 1 cm depth, the strongest correlations of wavelet transforms of decomposition with structural, microclimatic, and vegetation variables often differed in resolution from those dominant in the decomposition patterns. At the 4 cm depths, many of the strongest correlations occurred at the maximum resolutions examined. Although many important correlates differed between transects and depths within a transect, there were some consistencies. On both transects, surface and soil temperatures were strongly correlated ($|r| > 0.40$) with decomposition; soil temperatures were stronger correlates along the small block.

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The direction of association between decomposition and temperatures changed with depth, being negative at 1 cm and positive at 4 cm for both transects. Overstory was an important correlate ($|r| > 0.50$) for 3 of 4 transect-depth combinations. On both transects, correlations between decomposition and overstory peaked at different resolutions and were different signs (positive at 1 cm and negative at 4 cm) for the two decomposition depths. Along the pine barrens but not the small block, there were two peaks of resolutions of correlation that appeared consistently across variables. Thus, correlates of decomposition changed with scale as well as depth and management regime. This suggests that factors other than management may still be maintaining decomposition patterns on the landscapes. Further, patterns in and relationships to process variables should be examined at multiple scales to develop a comprehensive understanding of the mechanisms driving functional heterogeneity.

Das Verständnis der Landschaftsorganisation ist entscheidend für die Bestimmung der Auswirkungen von Management und für den Erhalt von strukturell und funktionell diversen Ökosystemen. Wir untersuchten die Beziehungen zwischen einer funktionellen Variablen, der Zersetzung, und mikroklimatischen, Vegetations- und Struktureigenschaften auf multiplen Skalen in zwei unterschiedlichen Landschaften im nördlichen Wisconsin, USA. Wir hofften, charakteristische Lösungen für Struktur-Prozeß-Beziehungen in den Landschaften aufzuklären, sowie die Gültigkeit von Extrapolationen von Struktur-Prozess-Beziehungen über Skalen und Management-Regimes zu bestimmen. Wir nutzten eine Kombination von ANOVA, „wavelet"-, kanonischer Diskriminanz- und Korrelationsanalysen und fragten uns insbesondere: (1) ob spezielle Kombinationen von mikroklimatischen, strukturellen und Vegetationseigenschaften durchweg mit Unterschieden in der Zersetzung zwischen den Managementzonen entlang der Transekte (d.h. innerhalb der Landschaften) verbunden waren; und (2) ob es bei verschiedenen Auflösungen der Analysen und Tiefen innerhalb und zwischen den Landschaften durchgängige Faktoren waren, die die Zersetzung beeinflußten. Die Zersetzung war in den beiden Landschaften in den Kieferödländern größer als in den „small block"-Transekten; und in 4 cm Tiefe größer als an der Oberfläche. Signifikante Unterschiede in der Zersetzung traten zwischen Management-„patches" sowohl für die Transekte als auch die Tiefen auf; mit Ausnahme der 4 cm Tiefe in den Kieferödländern. Im Allgemeinen war die Zersetzung in den „patch"-Typen mit größerer Oberholz-Deckung (overstorey) bei 1 cm schneller (beide Transekte), und bei 4 cm geringer („small block"-Transekt). Die Kanonische Diskriminanzanalyse trennte ebenfalls gemanagte „patches" nach der Oberholz-Deckung bei beiden Transekten. Sekundäre Vektoren) trennten ebenfalls „patches" nach dem Mikroklima, unabhängig vom Oberholz-Einfluss auf diese Variablen. Die dominanten Auflösungen in den Mustern der Zersetzung unterschieden sich zwischen den Transekten und Tiefen: 80 m (Kieferödländer, 1cm), 500 m (Kieferödländer, 4 cm), 160 m („small block"-Transekt, 1 cm) und 750 m („small block"-Transekt, 4 cm). Bei 1 cm Tiefe unterschieden sich die stärksten Korrelationen der „wavelet"-Transformation der Zersetzung mit strukturellen, mikroklimatischen und Vegetationsvariablen häufig in der Auflösung von denen, die dominant in den Zersetzungsmustern waren. Bei 4 cm Tiefe fanden sich viele der stärksten Korrelationen bei der maximalen betrachteten Auflösung. Obwohl sich viele, wichtige korrelierende Variablen (correlates) zwischen den Transekten und den Tiefen innerhalb eines Transektes unterschieden, gab es einige Gemeinsamkeiten. Auf beiden Transekten waren Oberflächen- und Bodentemperatur stark mit der Zersetzung korreliert ($|r| > 0.40$); die Bodentemperaturen waren die stärker korrelierenden Variablen entlang des „small block"-Transekts. Die Richtung der Beziehung zwischen der Zersetzung und der Temperatur änderte sich mit der Tiefe und war negativ in 1 cm und positiv in 4 cm Tiefe bei beiden Transekten. Oberholz war eine wichtige korrelierende Variable ($|r| > 0.50$) bei 3 von 4 Transekt-Tiefen-Kombinationen. Bei beiden Transekten erreichten die Korrelationen zwischen Zersetzung und Oberholz ihren Höhepunkt bei verschiedenen Auflösungen und zeigten unterschiedliche Vorzeichen für die beiden Zersetzungstiefen (positiv bei 1 cm, negativ bei 4 cm Tiefe). Entlang der Kieferödländer, jedoch nicht entlang des „small block"-Transekts, gab es zwei Höhepunkte der Auflösung der Korrelation, die bei den Variablen durchweg auftraten. Somit änderten sich die korrelierenden Variablen sowohl mit der Skala als auch mit der Tiefe und dem Management-Regime. Das legt nahe, dass andere Faktoren als das Management die Zersetzungs-Muster in den Landschaften aufrechterhalten. Weiterhin sollten Muster in und Beziehungen zwischen den Prozeß-Variablen auf multiplen Skalen untersucht werden, um ein umfassendes Verständnis der Mechanismen zu entwickeln, die die funktionelle Heterogenität vorantreiben.

Key words: Decomposition – scale – landscape function -– microclimate

Introduction

Much ecological research has considered the issue of inherent scales within nature, and many authors assert that ecological phenomena and relationships occur within distinctive ranges or domains of scale (e.g., Wiens 1989, Holling 1992). The components of scale define the spatial or temporal dimensions of an object or process (Turner & Gardner 1991) and inherent characteristics could be manifested in either or both components of scale, the resolution, i.e., the finest dimension measurable; or the extent, i.e., size of study area (spatial) or duration of study (temporal). In examining the scale-specificity of models and predictions, characteristic scales of structure and processes may emerge (Levin 1992). The strength of association between physical features on a landscape and the processes that are inferred to create these structures can further suggest inherent, natural scaling (Carlile et al. 1989). However, the scales at which heterogeneity is manifested for different physical and chemical properties or biological entities varies greatly (Dutilleul & Legendre 1993). Thus, the challenge is to reconcile dominant scales of patterns in one process or element with causal mechanisms that may differ in either temporal or spatial scale.

Decomposition is strongly associated with rates of nutrient cycling and thus soil productivity in different ecosystems (Jordan 1982, Vitousek 1982, Van Cleve et al. 1983, Waring & Running 1998) and is thus important to ecologists studying theoretical questions (e.g., productivity-stability relationships). Rates of decomposition are primarily related to climatic conditions and quality (i.e., chemical composition) of the organic matter. Specifically, these rates have been previously related to the direct and indirect influences of precipitation [e.g., contrast Latter et al. (1998) to Austin & Vitousek (2000)], interactions between temperature and precipitation (e.g., Cuevas & Medina 1986), potential evapotranspiration, actual evapotranspiration, and mean July temperature (Berg et al. 1993) and soil temperature and moisture (especially extremes of freezing, drought and water logging) (Oades 1988, Upadhyay et al. 1989), which both affect microbial activity (Berg 1986, French 1988). Site productivity, soil properties, soil depth, season, and overstory composition (i.e., microclimate and litter chemistry) have also been found to affect decomposition rates (Melillo et al. 1982, Nys & Howson 1988, Johansson 1994, Kochy & Wilson 1997). For example, Brown & Howson (1988) determined that decomposition was higher in stands of alder (*Alnus* spp.) and pine (*Pinus* spp.) than in stands of oak (*Quercus* spp.) or spruce (*Picea* spp.). There were also different interactive influences of climatic factors and depth among these forest types, possibly related to fine root morphology of the tree species or to differences among the stands in populations of macroinvertebrates (see also Mudrick et al. 1994).

Though much work has addressed the determinants of differences in decomposition rates among sites, the relative importance of variables in creating or maintaining functional heterogeneity at broader extents is not often examined (but see Kochy & Wilson 1997). Further, how these associations are altered by management (i.e., manipulations of landscape structure) or differ among landscapes is little understood. Litter quality (i.e., carbon:nitrogen ratio, lignin content) may play a greater role in organic matter decomposition within an ecosystem or habitat type (Taylor et al. 1989, Kochy & Wilson 1997) and may interact with landscape structure and microclimatic variables to influence decomposition (e.g., Mudrick et al. 1994, Fan et al. 1998). Litter composition may be particularly influential where microclimate differs little among habitats (e.g., Elliott et al. 1993). In contrast, climatic factors are relatively strong correlates of decomposition rates measured at coarse resolutions and regional extents (Meentemeyer 1978, Vitousek et al. 1994). At the intermediate extent, within or between landscapes, heterogeneity created by the juxtaposition of multiple management regimes may further confound any characteristic relationships among decomposition and structural or compositional features. Understanding these patterns in decomposition is relevant to managers in predicting productivity on the landscape or hoping to retain long-term productivity on harvested sites.

We undertook to examine the effects of scale (both resolution and extent) and management on landscape function using a standardized proxy for decomposition and proxies for many of the causal variables of interest. We focused our study of decomposition at the intermediate spatial extent, i.e., within a working forest that encompasses multiple management regimes. We then examined how consistent the relationships among ecosystem variables were across resolutions and management zones for this size of study area. We used two distinct landscapes in the Chequamegon National Forest to elucidate patterns in decomposition. To examine the consistency across resolutions of relationships between this functional variable and other ecosystem characteristics, we asked: 1) which combinations of microclimatic, structural, and vegetative features were associated with differences in decomposition among management zones of a landscape; and 2) which of these features explained variation in decomposition across scales within a landscape. We compared these associations between landscapes and depths, and among scales. The use of standardized material, cotton strips, to examine decomposition was

necessary to allow examination and comparison of this process across multiple ecosystem types and disturbance regimes. By thus controlling for both soil physical characteristics at the broad scale and the nature of organic material being decomposed, we attempted to determine only how management, and its influence on microclimate and landscape structure, would affect patterns of decomposition. By conducting this analysis at multiple scales, we hoped to detect any characteristic resolutions of structure-process relationships, and to determine the validity of extrapolation of structure-process associations across scales.

Materials and methods

Field Site

This study was conducted in the Washburn District of the Chequamegon National Forest (CNF), northern Wisconsin, USA (46° 30′–46° 45′ N, 91° 2′-91° 22′ W). The study area lies within subsection X.1, Bayfield Barrens, of the Regional Landscape Ecosystems of Wisconsin (Albert 1995). Soils are deep (30–90 m), loamy, glacial outwash sands with little organic material, classified as Psamments and Orthods. Underlying bedrock is Precambrian basalt, lithic conglomerate, sandstone, shale, and feldspathic to quartzose sandstone. Topography in the area ranges from level terraces to pitted outwash, formed by the melting of masses of glacial ice on which the sediments were deposited (CNF 1993, Albert 1995).

Our research was conducted within two landscapes (management zones) of the CNF, the pine-small block (SB) and the pine barrens (PB). We established two transects (one to sample each zone or landscape) that were similar in topography and underlying soils characteristics at the broad scale, both being in areas of level to pitted glacial outwash sands (CNF 1993). The transects were placed randomly within the landscapes after trying to control for these landform characteristics. At the patch level within transects, soil properties were similar within E and B horizons; however, some differences existed in pH and nutrient levels between the A horizons of hardwood and coniferous stands (Brosofske et al. 2001). The transects differed primarily in species composition and landscape-level structure defined by overstory vegetation. Management zones in the Washburn District are defined by "desired future condition" to provide a "healthy, functioning ecosystem" as determined by current managers (CNF 1993) based on an analysis of the pre-settlement vegetation, forest habitat types, and ownership of the surrounding land. Historically within the SB zone, frequent, naturally-occurring fires and burning by native Americans and early European settlers (Heinselman 1981) created a fragmented landscape. Current management promotes early and mid-successional species through harvesting in small patches of approximately 16 ha. Predominant overstory species are red pine (*Pinus resinosa* Ait.), planted during the 1940s, 70s and 80s, and jack pine (*P. banksiana* Lamb.), which has regenerated naturally. Species such as paper birch (*Betula papyrifera* Marsh.), red maple (*Acer rubrum* L.), trembling and big-toothed aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.), and red and northern pin oak (*Quercus rubra* L. and *Q. ellipsoidalis* E.J. Hill), occur due to natural successional dynamics and silvicultural activities. Along our transect, the management approach has produced a mosaic of small plantations of mixed pine at varying stages of development, and cutblocks harvested with different silvicultural treatments. There is no distinct matrix (i.e., no dominant patch type in terms of age or silvicultural approach) that can be visually identified based on current vegetation. Deciduous trees and shrubs exist within openings (usually landings or skid roads) created by harvesting.

The matrix along the pine barrens transect is relatively open, with clumps and scattered individuals of red, jack and white pine (*P. strobus*). Northern pin oak and hazelnut (*Corylus* spp.) are common understory shrubs. Predominant ground flora include sweet fern (*Comptonia peregrina*), blueberry (*Vaccinium* spp.), bearberry (*Arctostaphylos uva-ursi*), bracken fern (*Pteridium aquilinum*), and wintergreen (*Gaultheria procumbens*). Species distributions are highly dependent on the interaction between topography and fire, which is currently prescribed at a 5 to 10 year interval in order to maintain brush prairie areas for wildlife. Under this management regime, flat areas remain relatively open, north-facing slopes support more trees, primarily jack and red pine, and white pine is more common in lower frost pockets or seepage areas (CNF 1993, Brosofske et al. 1999). Areas that have not burned recently, adjacent to the open barrens, support dense *Corylus* scrub. Closed canopy stands consist of mixed pine-oak-maple or thick aspen.

We established a 3820 m linear, east-west transect within the SB management zone and a 2505 m transect through the PB. We defined 14 patch types along the SB transect (Tab. 1a) and eight patch types along the PB transect (Tab. 1b), based on overstory cover and species composition in the field, and examination of USDA Forest Service compartment records. Average patch width along the SB transect was 219 m (std = 212 m, max = 635 m, min = 20 m) and average slope was 7% (max = 34%, min = 0%). Patch width averaged 310 m along the pine barrens transect (std = 221 m, max = 645 m, min = 35 m) and average slope was 14% (max = 59%, min = 0%).

Table 1a. Location and descriptions of patch types and number of cotton decomposition strips along the pine small-block (SB) transect in Chequamegon National Forest, WI, from 0 m (west end) to 3820 m (east end). Data on height, age and diameter at breast height (DBH) are based on trees within a circular sample plot of 10 m radius (314 m^2). Cotton strips were not buried in roads identified below.

Code	Patch Name	Start (m)	End (m)	Strips (N)	Patch Description
P1	6yr Red Pine	0	65	7	originated 1989; height ≈ 1.5 m
P2	50yr Mixed Pine	70	230	16	mixed jack and red pine; 50 yrs; height ≈ 20 m, mean dbh = 24.9 cm (n = 17)
P3	Open w/ Scrub	235	365[a]	13	associated with old access rights-of-way and road edges
P4	60yr Red Pine	370	450	68	originated 1933; height ≈ 33 m , mean dbh = 29.6 cm (n = 10 dominants)
P5	Clearing	455	480	6	associated with old landings and access roads
P4	60yr Red Pine	485	505		as above
P5	Clearing	510	540		as above
P4	60yr Red Pine	545	1115[b]		as above
P6	Retention Jack Pine	1125	1745[c]	63	cut 1995; residual tree height ≈ 24 m, mean dbh = 29 cm (average 2 trees/ plot)
P7	7yr Red Pine	1755	1875	13	originated 1988; height ~ 2 m
P8	Clearcut w/ Slash	1880	2095	22	red pine stand cut 1993
P9	12 yr Red Pine	2100	2565	47	originated 1983; seedling-sapling >70% stocked in 1990; height ≈ 3 m
P10	Grassy Valley	2570	2795	23	100% grass cover, primarily *Carex* and *Oryzopsis*; scattered red pine ≈ 25 m height
P11	60yr Red Pine2	2800	2920	12	originated 1934; height ≈ 28 m, mean DBH = 31.6 cm (n = 9 dominants)
P12	Clearcut	2925	3560[d]	64	recently cut red pine sawtimber stand
P13	50yr Red Pine2	3570	3670	10	height ≈ 22.1 m, average dbh = 25.1 (n = 31)
P14	50/30yr Mixed Pine	3675	3820	15	jack pine height ~≈ 22.0 m, mean DBH = 13.1 cm, age ≈ 50 yrs (n = 8); red pine height ≈ 12 m, mean DBH = 10.1 cm, age ≈ 30 yrs (n = 27)

[a] sand road at m 255
[b] ATV trail at m 780; atv trail at m 1085–1090; sand road at m 1120
[c] ATV trail at m 1450; gravel road at m 1750
[d] gravel road at m 3565

Table 1b. Location and descriptions of patch types and numbers of cotton decomposition strips along the pine barrens (PB) transect in Chequamegon National Forest, WI, from 0 m (west end) to 2515 m (east end). Data on height, age and diameter at breast height (dbh) are based on trees within a circular, sample plot of 10 m radius (314 m^2). Cotton strips were not buried in roads identified below.

Code	Patch Name	Start (m)	End (m)	Strips (N)	Patch Description
P1	Pine/Oak/Maple Stand	0	160[a]	13	originated 1940; burnt 1994; height ≈10 m; red maple mean dbh = 8.6 cm (n = 9); pin oak mean dbh = 11.5 cm (n = 26)
P2	Upland Scrub	175	495	33	*Corylus* and *Quercus* shrub, ~ 1.5 m height
P3	Aspen Copse	500	535	4	dense *P. tremuloides* with *Corylus* understory
P4	Open Pine Barrens	540	1060	52	*Comptonia peregrina* and *Vaccinium* spp. ground layer; scattered red and jack pine
P5	Upland Brush	1065	1725[b]	63	pine barrens with *Populus* scrub; nonstocked
P6	Aspen Scrub	1730	1920[c]	18	*P. tremuloides*; cut 1989
P7	Populus Stand	1925	2420[d]	48	age = 22 yrs, height ~ 8 m, mean dbh = 8.2 cm (n = 76)
P8	Populus/Acer Stand	2425	2515	10	*P. tremuloides* and *A. rubrum* height ~ 10 m

[a] old access road m 65; gravel road at m 165–170
[b] old landing m 1080–1100, old access roads m 1175 and 1565
[c] sand road m 1825
[d] old skid road m 1945—1960

Decomposition Strips

We used Shirley Soil Burial Test Fabric (unbleached, commercial, cotton calico) to assess organic decomposition rates associated with microbiological activity (e.g., Sagar 1988) along the transects in 1996. Two 12 cm × 20 cm strips were buried, using a flat-edged shovel, in random locations within 1 m^2 plots placed every 10 m along the transects starting at 5 m. We thus had a total of 382 plots (764 strips) along the SB transect and 251 plots (502 strips) along the PB transect. Strips were buried vertically with minimal (~ 3 cm) overlap at the bottom, and ~ 3 cm remaining above the mineral soil surface. We buried strips on June 10 and 11 and removed them on July 14 and 15, 1996. It is desirable to remove strips after a substantial (> 50%) decrease in strength has occurred but before a loss of 85% strength has been reached, at which point strips are difficult to remove undamaged from the soil (Latter & Howson 1977). The length of the burial period we used was based on pilot studies conducted in the same landscapes during 1995. Thirty-one small-block

strips and six pine barrens strips could not be relocated or were too decomposed to be retrieved. We felt influences on subsequent analyses would be minimal due to our large sample size, particularly along the SB transect. Thirty-five strips were also buried and removed immediately to provide control measurements of tensile strength. We marked the level of the mineral soil surface on each strip with permanent marker prior to removal and placed each strip in a separate paper bag for transport.

Cotton strips were oven dried at 65 °C until completely dry (approximately 10 hours). We cut and then frayed the strips into 1 cm widths from 0–1 cm, 3–4 cm, and 6–7 cm depths. Tensile strength ($KN \cdot m^{-1}$) of these substrips was measured using a Scanpro Alwetron TH- strength tester. All strips were stored at constant humidity with the strength tester for at least 24 hrs prior to testing. Tensile strength for each substrip was recorded as a loss relative to the average of the strengths of the 35 control strips. Substrips that were too decomposed to register a tensile strength ($\approx 0.50\ KN \cdot m^{-1}$) were assigned 0 values.

Temperature, Landscape Structure and Soil Moisture

We measured soil temperature at 5 cm depth (°C; T_s) and air temperature at soil surface (°C; T_{sf}) at the center of the same plots within which decomposition strips were buried (every 10 m) using a set of mobile climatic stations. The PB transect was monitored between June 10 (Julian day 161) and September 24 (Julian day 267) 1994. The SB transect was monitored between June 12 (Julian day 163) and August 25 (Julian day 237) 1995. Temperatures were measured every 20 seconds and averaged and recorded every 15 minutes. We maintained two reference microclimate stations, one in a closed canopy pine/oak stand in the Moquah Research Natural Area (REFC) and one in the open pine barrens (REFO), continuously during the 1994 and 1995 study seasons. These provided data from the extremes of canopy cover and enabled us to develop predictive relationships between temperature at reference locations and at points along the transects (see below).

We assessed landscape structure (patch type) and vegetative cover within the 1 m^2 quadrats (every 10 m). We recorded patch type (Tab. 1) and percent cover of overstory vegetation (using spherical canopy densiometer), vegetation > 0.5 m high (excluding overstory), vegetation < 0.5 m high, and litter. We also measured depth of the undecomposed litter (duff, cm) at the center of each plot. Vegetation measurements for the pine barrens transect were done in 1994 and measurements for the small-block transect were completed in 1995, i.e., during the same years that temperature was measured for each transect respectively. Elevation was determined prior to leaf-out in spring of 1997 for 0–1500 m of the SB transect, and the entire PB transect using a Leica TC 600 laser total laser station. A measure of relative microtopography (relmicro) was calculated as:

$$relmicro = x_i - \bar{x}_{(i-3 \ldots i \ldots i+3)} \quad (1)$$

where x_i is the elevation of point i; relative position of a point on the landscape (relmacro) was determined as:

$$relmacro = x_i - x_{min} \quad (2)$$

where x_{min} is the elevation of the lowest point on the transect. Absolute elevation is between 360 and 400 m along both transects.

We determined soil moisture (volumetric water content) during 1997 (June 21, PB; June 22, SB) at each site at which cotton decomposition strips had been buried. Although moisture was measured during a different growing season, we expected that moisture patterns would be similar across the landscapes between years, allowing us to detect associations with structural features and decomposition. A subset of points (N = 150) measured along both transects in 1996 showed a high correlation with measurements in 1997 ($r^2 > 0.70$). Volumetric water content was determined by Time Domain Reflectometry (TDR) using a Model 6050X1 Trase System (Soilmoisture Equipment Corp.) with 10 cm long soil probes using the methods of Gray & Spies (1995). We calculated percent volumetric water content from equations of Gray & Spies (1995) for sites with the lowest percent organic content and highest percent sand (characterized as sandy loams) in their study.

Analysis

Temperature Standardization

We replaced missing data (due to equipment damage by animals, equipment failure, data overwrite, or inability to measure temperature on active roads or ATV trails) by: 1) averaging temperatures from time periods or spatial locations on either side of a single missing point; or 2) developing simple linear regression equations based on temperatures measured at adjacent or nearby points, or at the reference stations, for larger spatial or temporal data gaps. Gaps of 0.25–3.0 hours for a single point in space occurred on average six times per original measurement period (11–14 days). Gaps of more than one hour in duration or two sampling points in distance occurred less frequently (three to four times in the time period over which an entire transect was measured).

We determined average temperature at each point along the transect during the morning (05:00–10:45 hrs), midday (11:00–16:45 hrs), evening (17:0– 22:45 hrs), and night (23:00 hrs, day_{t-1}–04:45 hrs, day_t). We then standardized our data to produce a series of values as though all points had been measured concurrently (see Saunders et al. 1998 for details of methodology). These standardized data were used in all subsequent analyses.

Statistical Analysis

First we examined whether management at the broad, transect extent had any influence on decomposition by depth. We tested for significant effects of transect (2), strip (2) and depth (3), and 2-way interactions between these factors on loss of tensile strength (CLTS) using ANOVA in SAS. As there was no significant difference in mean CLTS between strips ($p > 0.40$) and no difference in distribution of decomposition values between strips for any transect-depth combination (Kolmogorov-Smirnov Goodness of Fit, $p > 0.30$), subsequent analyses utilized that strip from which the most substrips were available. We used one-way ANOVA to reexamine the effects of depth on CLTS by transect. Only CLTS1 (CLTS between 0 and 1 cm) and CLTS4 (CLTS between 3 and 4 cm) were examined further due to lack of significant difference between depths of 4 and 7 cm ($p > 0.05$). Based on low Pearson correlations ($r < 0.20$) between CLTS1 and 4 for each transect, we chose to analyze decomposition patterns separately for each depth along each transect.

Second, we asked whether within-transect management activities produced patches of decomposition of finer extent. ANOVA (GLM procedure for unbalanced designs in SAS; SAS Institute 1990) was used with post-hoc Bonferroni t-tests to examine differences between decomposition levels in the original data at both 1 cm and 4 cm depths among management patch types. Only patch types with $N \geq 10$ were included. Thus, P3, aspen copse, was removed from this analysis along the PB transect and patch types 1 (6 yr red pine) and 5 (small clearings) were removed along the SB transect.

We then used canonical discriminant analysis (CDA) to assess which suites of microclimatic, structural, and vegetative variables were related to the decomposition differences among patches along each transect at the 1 cm and 4 cm depths. We examined parallels between differences among patches in decomposition (from ANOVA above) and the separation of patches along structural-microclimatic-vegetative axes produced by the CDA. Variables used in the analysis included: relative microtopography (relmicro), relative macrotopography (relmacro), a slope*aspect interaction variable (calculated as (slope %*cos (aspect-45)); Stage 1976), slope, surface temperatures (morning, midday, evening, night), soil temperatures (morning, midday, evening, night), soil moisture, overstory cover, litter cover, and duff depth. All percentages were arcsine transformed for normalization.

Lastly, we used wavelet and correlation analysis to examine the structure/microclimate/vegetative-decomposition relationships at the broad, transect level and to assess the effects of resolution on the relationships at this extent. Wavelet analysis approximates a data series as a linear combination of functions with specific resolutions and locations. Thus, the technique quantifies the pattern within a data series as a function of scale (resolution) and location along a transect and indicates the dominant scales of pattern in a dataset (Bradshaw 1991, Graps 1995, Dale & Mah 1998). Wavelet analysis also confers a distinct advantage over other techniques used for detection of pattern and dominant scales, e.g., Fourier analysis, in that it does not require stationary data. We calculated wavelet transforms for CLTS at 1 cm and 4 cm depths and all variables used in the CDA along both transects with the program of Li & Loehle (1995). The wavelet transform is defined in discrete form as:

$$W(a,b) = \frac{1}{a}\sum f(x)\cdot g\left(\frac{x-b}{a}\right) \qquad (3)$$

where the shape (i.e., the dimension of the window of analysis) of the analyzing wavelet, $g(x)$, changes with scale, a, and the analyzing wavelet moves along the data series, $f(x)$, centered at each point, b, along the transect (Bradshaw & Spies 1992, Li & Loehle 1995). The wavelet transform was calculated across scales of a = 10, 20..., 750 in $a \leq b \leq$ n-a, for x = 5, 15,...n, n = 3815, along the small block transect and a = 10, 20..., 500 in $a \leq b \leq$ n-a, for x = 25, 35...n, n = 2505 through the pine barrens landscape. We used the wavelet variance, $V(a)$:

$$V(a) = \frac{1}{n}\sum W^2(a,b) \qquad (4)$$

associated with the wavelet transforms for each transect and depth to reveal any dominant scales contributing to the overall pattern of decomposition at both depths across this landscape (Bradshaw 1991). We correlated the transforms of all structural, microclimatic, and vegetative variables with transforms of both decomposition variables (1 cm and 4 cm depths) at scales of 10–500 m by 10 m along the pine barrens and 10–750 m by 10 m along the small block transect. We compared the variables which correlated most strongly ($|r| > 0.30$) with decomposition and the dominant scales of these correlations between the depths within a transect and between transects.

Results

The main effects of transect and depth, and an interaction effect of transect*depth all had significant influences on cotton loss of tensile strength ($p < 0.0001$) and together explained a total of 59% of the variation in CLTS ($F = 911.37$, $p < 0.0001$). Along both transects analyzed separately, CLTS differed significantly ($p < 0.05$) between the 1 cm and 4 cm depths. Mean decomposition was greater at 4 cm than at the 1 cm depth along both transects ($p < 0.0001$), and greater at both depths for the PB than the SB transect ($p < 0.0001$). CLTS ranged from 3.43 $KN \cdot m^{-1}$ (stdev 4.60) and 5.67 $KN \cdot m^{-1}$ (stdev 5.10) for the small block and pine barrens respectively at 1 cm, to 12.53 $KN \cdot m^{-1}$ (stdev 2.03) and 13.53 $KN \cdot m^{-1}$ (stdev 1.33) for the small block and pine barrens respectively at 4 cm (Fig. 1).

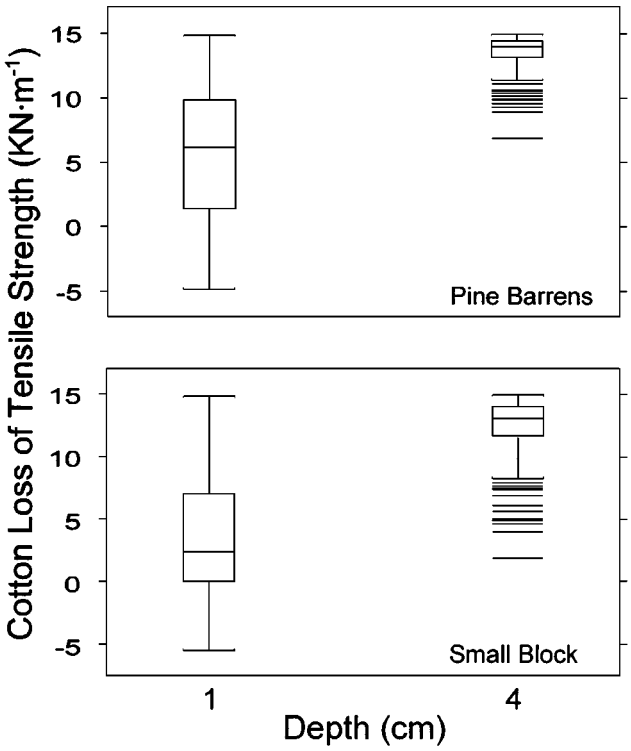

Fig. 1. Boxplots of decomposition (Cotton Loss of Tensile Strength, CLTS, $KN \cdot m^{-1}$) at 1 and 4 cm depths along the pine barrens (N = 249) and small-block (N = 380) transects in the Chequamegon National Forest, WI. Boxes indicate the median (solid line inside box) and the distance between the upper and lower quartiles (IQD, upper and lower ends of the box). Whiskers indicate a distance of 1.5*IQD and outliers are shown by horizontal lines.

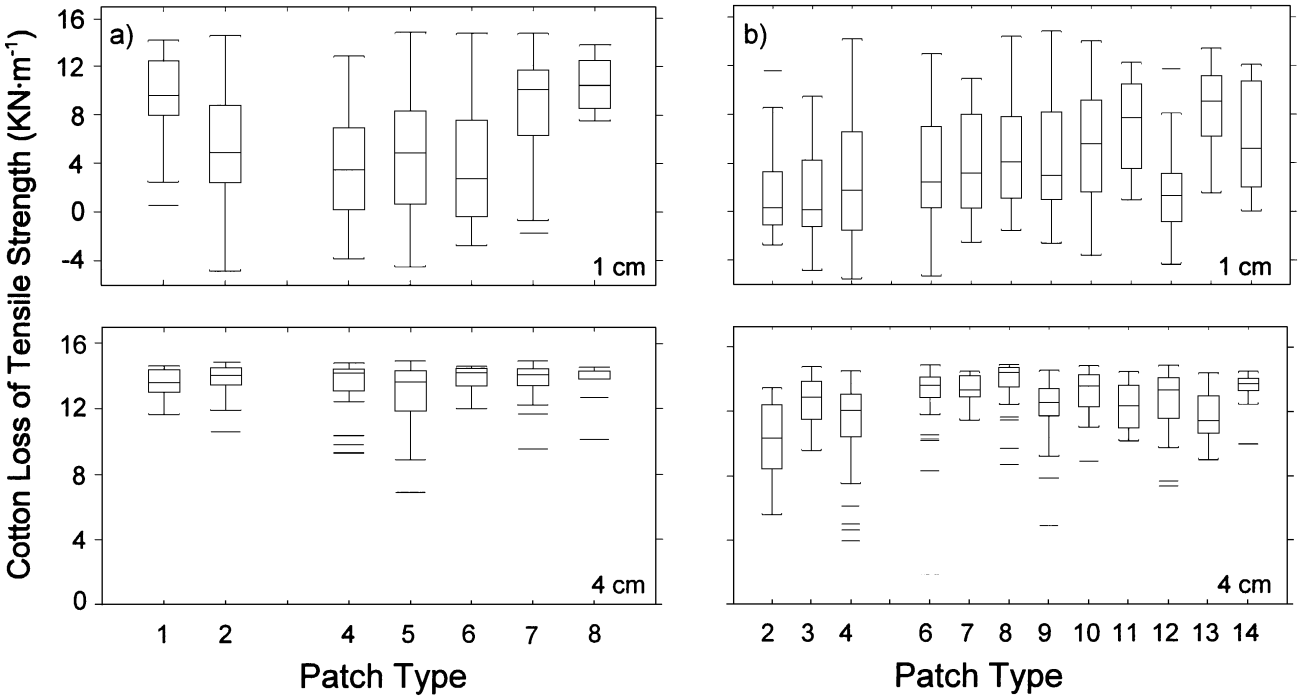

Fig. 2. Boxplots of decomposition (Cotton Loss of Tensile Strength, $KN \cdot m^{-1}$) at 1 and 4 cm depths for management patches along A) the pine barrens and B) the small block transects in the Chequamegon National Forest, WI. For the pine barrens transect, N = 13 (P1), 33 (P2), 52 (P4), 63 (P5), 18 (P6), 48 (P7) and 10 (P8)). For the small block transect, N = 16 (P2), 13 (P3), 68 (P4), 63 (P6), 13 (P7), 22 (P8), 47 (P9), 23 (P10), 12 (P11), 64 (P12), 10 (P13), and 15 (P14). See Fig. 1 for details of boxes and Table 1 for description of patches. Only those patches for which $N \geq 10$ are included in analyses.

Along the pine barrens transect, mean CLTS at the 1 cm depth in management patches P1 (pine/oak/maple stand), P7 (22 year old aspen), and P8 (aspen/maple stand) showed the largest ($p < 0.05$) differences from other patch types, all three having relatively higher rates of decomposition (Table 2a; Fig. 2A). No significant differences in decomposition ($p > 0.05$) were noted among management patch types at the 4 cm depth for this transect (Table 2a; Fig. 2A). Along the small-block transect, there were significant differences in both CLTS1 and CLTS4, though these did not occur for the same sets of management patches. Patch types 12 (clearcut) and 13 (one of the 50 yr old red pine stands) differed most at the 1 cm depth, with the clearcut having relatively low and the 50 yr pine stand having relatively high decomposition levels. Mean decomposition in patch types 2 (another 50 year old red pine) and 4 (60 yr old red pine) differed most at the 4 cm depth, with relatively low levels of decomposition (Table 2b, Fig. 2b), though the median value was also low for patch type 13 (Fig. 2b).

Canonical discriminant analysis of structural, microclimatic, and vegetation characteristics along the pine barrens indicated significant differences in values of the canonical variables among the management patch types (Wilk's Lambda = 0.012, Pillai's Trace = 3.17, $p < 0.0001$). There were some consistencies between transects in the suite of characteristics that most differentiated patches (Tab. 3). Although Likelihood Ratio (LR) tests suggested that six of the canonical correlates were significantly different from 0 (LR = 0.889, F = 2.487, $p < 0.006$), graphical analysis indicated that only two variables separated management patches distinctly, and subsequent interpretation was restricted to these vectors. Positive values along canonical vector 1 of the pine barrens ($CV1_{pb}$) appeared to represent points of relatively high overstory cover and low relative microtopography (Tab. 3). This vector divided the management patches into two groups, patches 1, 7, and 8 versus 2, 4, 5, and 6 (Fig. 3). Canonical vector 2 ($CV2_{pb}$) separated patches 2 and 4 most distinctly along a microclimatic gradient, being correlated primarily with soil and surface temperatures in the evening and night time (Tab. 3). Along the small-block transect, seven canonical correlates were significantly different from 0 (LR = 0.876, F = 1.462, $p = 0.047$).

Table 2. Results of Bonferroni T-tests of decomposition levels among management patch types along A) the pine barrens (PB) transect, and B) the pine small-block (SB) transect, Chequamegon National Forest, WI. "1" indicates a significant difference between two patches at 1 cm depth; "4" indicates a significant difference at the 4 cm depth. See Tables 1a and 1b for description of patch types.

a)

Patch Type	Patch Type						
	1	2	4	5	6	7	8
1							
2							
4	1						
5	1						
6	1						
7		1	1	1	1		
8			1	1	1		

b)

Patch Type	Patch Type											
	2	3	4	6	7	8	9	10	11	12	13	14
2												
3												
4												
6	4		4									
7	4											
8	4		4									
9	4											
10	4		4									
11												
12	4		4						1			
13	1	1	1							1		
14	4		4							1		

As above, interpretation was restricted to the first two canonical variables based on limited graphical separation among patch types by the other vectors. Canonical vector 1 ($CV1_{sb}$) was most strongly and negatively associated with overstory cover, and $CV2_{sb}$ was primarily a variable combining surface temperatures across times of the day (Tab. 3). Separation of patch types was not as distinct for the small-block as for the pine barrens transect. However, the patch types that differed most in decomposition levels (see Tab. 2b) were, generally, those with relatively high overstory cover (more negative values along the *x* axis in Fig. 3), similar to results for the pine barrens transect.

Wavelet variances suggested two dominant scales (i.e., average distance between the center of a gap and center of a patch; Dale & Mah 1998) in the pattern of decomposition along the PB transect at the 1 cm depth; 10 m and 80 m (Fig. 4). Resolutions greater than 390 m also appeared to influence the pattern strongly. At the 4 cm depth, the wavelet variance dropped abruptly after the 10 m resolution, and then increased again to the maximum analyzed, 500 m. Along the SB transect, characteristics of the wavelet variances of decomposition displayed some similarities to the pine barrens (Fig. 4). At the 1 cm depth, there were two distinct peaks (10 m and 160 m), though the wavelet variance decreased after this point, unlike that for the PB at this depth. At the 4 cm depth, the small-block wavelet variance was also prominent at the 10 m resolution and increased to the coarsest analysis, 750 m.

Examining correlations between wavelet transforms and the microclimate, structure, and vegetative variables along the pine barrens at 1 cm depth, the strongest negative associations were with early surface and afternoon soil temperatures (Tab. 4, Fig. 5). There were strong positive correlations with moisture, overstory cover, duff depth, and microtopography. Strongest associations occurred at scales > 400 m, though there was a distinct second peak of association between 140 and 190 m (e.g., overstory, duff, Tab. 4, Fig. 5). In some cases, the same variable had different signs of correlation at different scales, e.g., duff, r = 0.47 at 500 m and

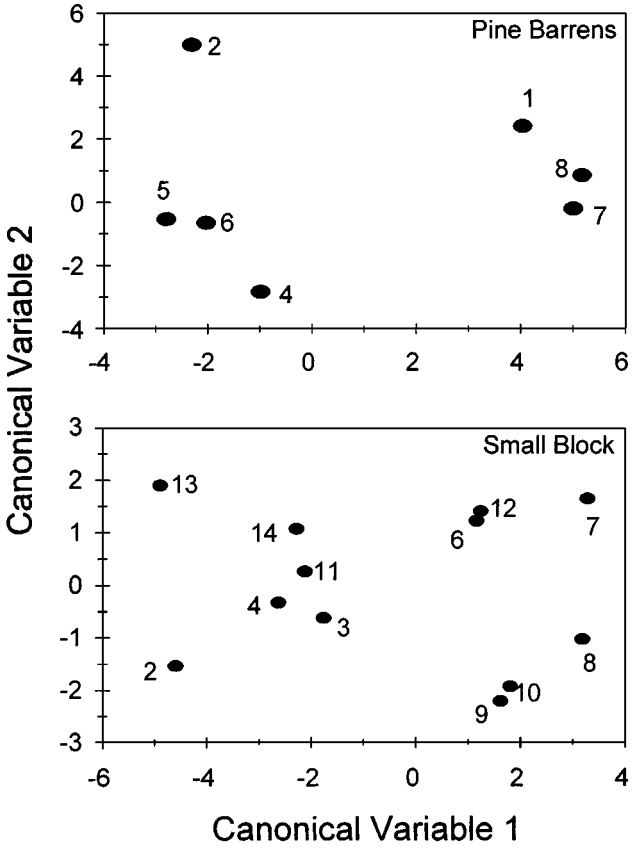

Fig. 3. Position of management patches along canonical vectors 1 and 2 from canonical discriminant analysis among structural, vegetal, and microclimatic characteristics of patches along the pine barrens (PB) and small block (SB) transects in the Chequamegon National Forest, WI. See Table 3 for standardized canonical coefficients and Table 1 for description of patches.

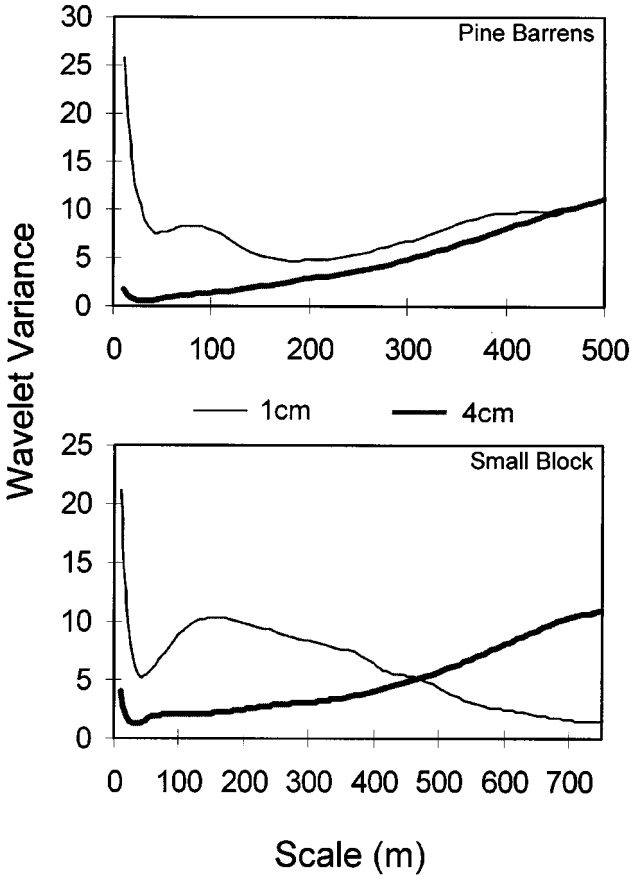

Fig. 4. Wavelet variances from wavelet transforms of decomposition (CLTS, $KN \cdot m^{-1}$) at 1 and 4 cm depths along the pine barrens (PB) and small block (SB) transects in the Chequamegon National Forest, WI.

Table 3. Standardized canonical coefficients for canonical variables (CV) from canonical discriminant analysis of structural, vegetation and microclimatic variables among management patches along the pine barrens (PB) and small-block (SB) transects, Chequamegon National Forest, WI.

Variable	Standardized Coefficient			
	PB		SB	
	CV1	CV2	CV1	CV2
Macrotopography (m)	0.105	0.096	NM[a]	NM
Microtopography (m)	–0.677	1.301	NM	NM
Aspect*Slope	–0.031	–0.050	0.116	–0.102
Slope (%)	0.038	0.054	0.295	–0.192
Tsf[b] (morning, °C)	0.095	0.305	0.476	0.011
Tsf(midday, °C)	–0.106	–1.016	–0.352	0.888
Tsf (evening, °C)	0.120	2.086	0.296	–0.548
Tsf (night, °C)	0.108	–2.417	–0.265	1.470
Ts[c] (morning, °C)	–0.447	–0.818	0.444	0.419
Ts(midday, °C)	0.210	1.318	–0.490	0.002
Ts (evening, °C)	0.024	–2.472	0.262	–0.338
Ts (night, °C)	0.233	2.411	–0.181	0.484
Moisture (%)	–0.128	0.183	–0.088	0.023
Vegetation <0.5 m (%)	NM	NM	–0.183	–0.292
Vegetation >0.5 m (%)	NM	NM	0.006	0.120
Overstory (%)	3.061	0.117	–2.165	–0.335
Litter (%)	0.045	0.139	0.269	0.280
Duff (cm)	–0.018	0.097	–0.086	0.120

[a] not measured
[b] air temperature at the soil surface
[c] soil temperature at 5 cm depth

Table 4. Maximum correlations (scales at which maximum correlations occur, m) between wavelet transforms of decomposition (cotton loss of tensile strength, $KN \cdot m^{-1}$) at 1 and 4 cm depths and transforms of topographic, microclimatic, and vegetation variables along the pine barrens (PB) and small-block (SB) transects, Chequamegon National Forest, WI. Correlations were examined at scales of 10–500 m by 10 m increments along the PB transect and at 10–750 m by 10 m along the SB transect.

Variable	Correlation (r)			
	PB (1 cm)	PB (4 cm)	SB (1 cm)	SB (4cm)
Microtopography	0.32 (100)	–0.30 (160)	NM[a]	NM[a]
Macrotopography	0.16 (70)	–0.40 (350)	NM	NM
Slope*aspect	–0.17 (170)	0.32 (450)	–0.44 (460)	0.34 (170)
Slope (%)	–0.20 (160)	–0.44 (170), –0.43 (370)	0.60 (720)	–0.26 (290)
Tsf[b] (morning, °C)	–0.49 (430)	0.46 (420)	–0.51 (430)	0.56 (740)
Tsf (midday, °C)	–0.54 (500), –0.32 (150)	0.50 (420)	–0.48 (390)	0.60 (740)
Tsf (evening, °C)	–0.50 (390)	0.33 (500)	0.28 (670)	0.76 (740)
Tsf (night, °C)	0.34 (140)	–0.26 (310)	0.29 (280)	0.56 (740)
Ts[c] (morning, °C)	0.24 (160)	0.42 (180), 0.42 (500)	–0.44 (750)	0.43 (740)
Ts (midday, °C)	0.22 (180)	0.35 (160)	–0.45 (750)	0.57 (750)
Ts (evening, °C)	–0.42 (490)	0.30 (180)	–0.44 (750)	0.61 (750)
Ts (night, °C)	–0.40 (450)	0.25 (500)	–0.34 (750	0.59 (740)
Moisture (%)	0.79 (500)	0.20 (500)	–0.21 (170)	–0.14 (110)
Vegetation < 0.5m (%)	NM	NM	–0.26 (630)	–0.26 (630)
Vegetation > 0.5m (%)	NM	NM	0.20 (480)	–0.34 (750)
Overstory (%)	0.76 (490), 0.55 (160)	–0.27 (370)	0.61 (750)	–0.51 (330)
Litter (%)	0.24 (500)	0.51 (500)	0.18 (240)	0.26 (740)
Duff (cm)	0.47 (500), –0.26 (190)	0.43 (390), 0.41 (490)	0.34 (750)	0.20 (130)

[a] not measured
[b] air temperature at the soil surface
[c] soil temperature at 5 cm depth

r = –0.26 at 190 m. At the 4 cm depth along the pine barrens, correlations between decomposition and soil and surface temperatures early in the day were still strong but were positive, in contrast to those at the 1 cm depth. Moisture and overstory did not appear to be important correlates of decomposition at 4 cm. Duff was still a strong correlate, and measures of macrotopography and slope became stronger correlates at this depth. Two peaks of correlation between decomposition and other variables were still apparent at approximately 170 m and > 400 m scales (e.g., slope and morning soil temperature, Tab. 4). On the SB transect, similar to the PB, both early surface temperatures and soil temperatures were strong correlates of decomposition, soil being stronger along the small block. The direction of association between decomposition and temperatures changed with depth, being negative at 1 cm and positive at 4 cm (Tab. 4) along this transect. Correlations between decomposition and overstory along the SB peaked at different scales and were different signs (positive at 1 cm and negative at 4 cm) for the two decomposition depths (Fig. 5), also similar to the PB. Unlike the PB, there were not two peaks of scales of correlation that showed up consistently across variables. Many of the strongest correlations occurred at the maximum resolution examined, 750 m.

Discussion

Estimates of ecosystem processes, such as decomposition, nutrient cycling or primary production, or population process such as dispersal, can be difficult to acquire across broad and multiple scales. Patterns are not often studied intensively at the landscape level due to the impracticalities of sampling (e.g., Frantzen & van den Bosch 2000). However, management activities such as forestry and regional development can alter landscape patterns and pattern-process relationships at many levels. Different variables may be necessary to predict or explain variation in ecosystem processes at landscape versus finer scales (Turner 1989), and understanding the validity of extrapolating relationships from one scale to another is vital for developing predictive models of ecosystem dynamics. Sustaining structural and functional diversity on managed landscapes requires assessment of the scales at which spatial heterogeneity has a significant influence on ecosystem function, and determination of the driving processes at different scales.

Organic decomposition is primarily controlled by the activity of microbiotic organisms (Escher et al. 2000), which is in turn influenced by heat and moisture availability (Olson 1963) and litter quality (Fogel

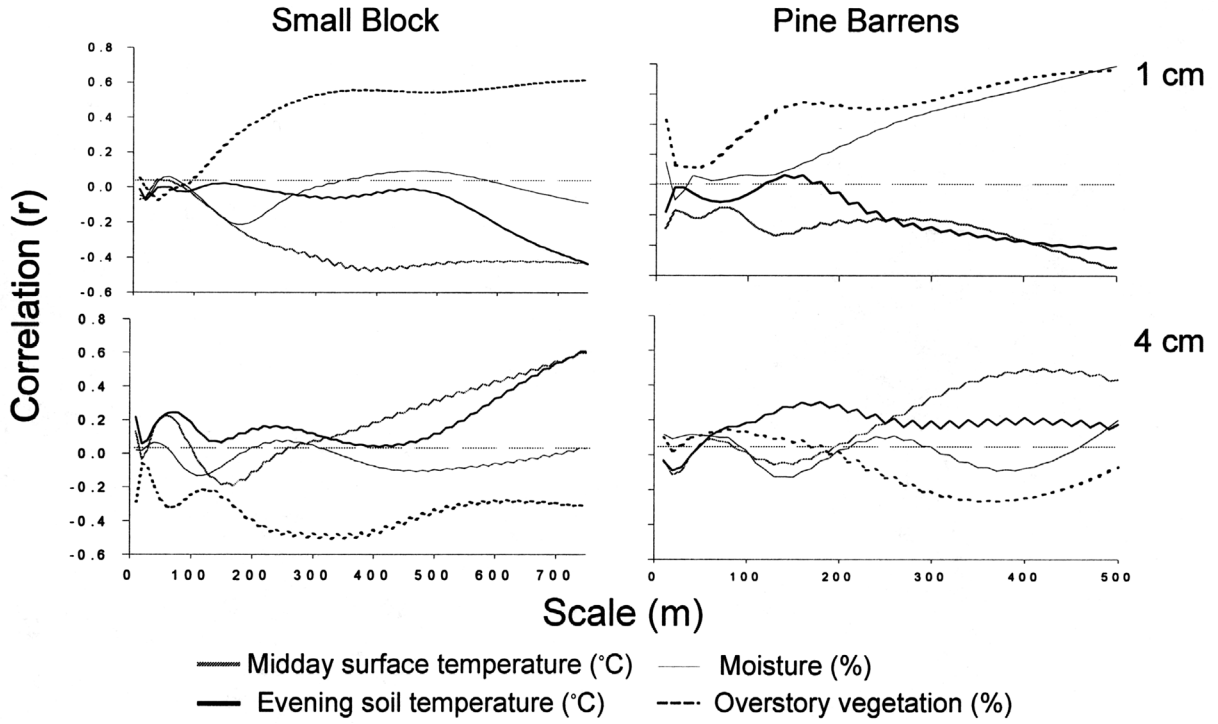

Fig. 5. Correlations between wavelet transforms of decomposition (CLTS, KN · m^{-1}) at 1 and 4 cm depths with midday surface temperature, evening soil temperature, soil moisture, and overstory cover. Correlations are shown at scales of 10–750 m every 10 m along the small block and 10–500 m every 10 m along the pine barrens transect.

& Cromack 1977). However, the relative importance of these regulating factors varies with the spatial extent of analysis. Meentemeyer (1978, 1984) examined the spatial variation in decomposition rates among sites across both continental and regional extents. At the continental level, actual evapotranspiration (ET), a measure of energy and moisture availability, explained up to 80% of the variation in decay rates. As the spatial extent of study was reduced, chemical and physical properties of litter material became more important determinants of decay rates. At the stand level, microclimatic differences among sites have been cited to explain high variation in the importance of coarse-scale soil climatic variables (e.g., Berg et al. 1984).

Components of temporal scale also exert strong influences on conclusions regarding control of ecosystem processes. For example, Anderson (1992) determined that mean annual soil temperatures at 0–4 cm depth ($r^2 = 0.81$) and mean annual ET ($r^2 = 0.50$) were most important in explaining mass loss of litter on a yearly basis, i.e., resolution, in northwestern Europe. However, regression models for mass loss on a daily basis incorporating soil temperature and soil moisture were a relatively poor fit. Coarser resolution trends were confounded by microclimatic variation. When examining multiple sites across a broad extent (2000 km) and long temporal duration (> 1 yr), Johansson et al. (1995) found that the relative importance of climate and litter composition in regulating decomposition changed as decomposition progressed. Climatic variables (ET) were dominant regulators in the first year and a combination of lignin concentration and climate was important after > 20% mass loss had occurred.

We expected that, at the landscape extent, temperature and soil moisture would be the primary correlates of decomposition rates. Although our temporal duration was relatively short (approximately six weeks during the growing season), our measures of climate were specific to the landscapes, rather than derived from regional macroclimatic measurements, and effects of litter quality were controlled through the use of the cotton strip assay. We further predicted topography to be an important determinant of decay and to impose definite structure on the scale of decomposition patterns in the pine barrens. Thus, we expected the scales at which patterns in decomposition were manifested might be relatively more influenced by topography than management along the PB, a more rolling landscape, whereas distinct zones of decomposition would parallel management patches to a greater extent along the SB transect. Within a landscape, effects of management activities on decomposition were anticipated to manifest themselves in differences among patch types.

Overstory coverage was an important predictor of decomposition in this region, as shown by the correlations of the wavelet transforms. Regardless of landscape type, overstory was also the dominant correlate of canonical variables for both transects (also microtopography for the PB). The species of overstory maintained on the landscape can influence microbial activity and physical properties of the soil (Nys & Howson 1988). This role may be imposed through an integrative influence of overstory on both moisture and soil temperature, or through other effects on soil properties, either chemical or physical. Although CDA indicated a limited role of temperature in differentiating management patches, overstory cover may have mediated decomposition through integrated, longer-term effects on radiation and precipitation reaching the ground than were otherwise recorded (e.g., see Kurka et al. 2000). Overstory coverage may also act as a proxy for actual evapotranspiration, shown to correlate strongly with decomposition in forest systems (Kurka et al. 2000).

The dominant variation in decomposition was at the surface in the PB and at 4 cm in the SB transect (Tab. 2). Along the small block transect, older stands (50 and 60 years old) generally had slower rates of decomposition at 4 cm depth than younger plantations, open areas and clearcuts of different ages. Decomposition in the retention jack pine site was higher than in some 50 yr (P2) and 60 yr (P4) stands but not higher than in clearcuts and other open areas. Thus, the subsurface environment created by this level of overstory retention did not appear to maintain processes at a pre-harvest level. Clearcuts may have exhibited higher below-surface decomposition rates due to increases in temperature at this depth relative to closed-canopy areas (Keenan & Kimmins 1993). For example, patch 12, the largest clearcut on the small-block, had a mean midday soil temperature of 20.01 °C (std = 3.34) as compared to 13.08 °C (std = 1.44) in 50 yr mixed pine (P2) and 16.41 (std = 3.13) in 60 yr red pine (P4). Similarly, Binkley (1984) found that decomposition below the surface in clearcuts in coastal temperate rainforest was greater than in uncut areas. Temperature effects could similarly explain the slower decomposition at the surface of the P12 clearcut, as compared to older pine stands P13 and P14. In relatively warm climates, decomposition can be inhibited at the ground surface within clearcuts due to extreme temperatures and desiccation (e.g., Kirmse et al. 1987). Prescott (1997) also demonstrated higher rates of decomposition in old growth than cut areas in montane ecosystems where summer moisture is critical for decomposition. These effects of surface environment were apparent in the pine barrens where patches with overstory cover (saplings or larger) had significantly faster decomposition rates at the surface than areas of open pine barren or scrub/brush. Thus, decomposition may be moisture limited along the PB transect but temperature-limited along the SB transect, where overstory coverage is relatively greater. Overstory may, therefore, be acting as a surrogate for the integrated effects of microclimatic variables on decomposition. Managers should be aware that overstory manipulation plays an ecologi-

cally significant role in altering below-ground processes not only through direct pathways (e.g., litter composition and quality; see below) but also through these indirect, abiotic mechanisms.

Alternatively, factors such as higher soil acidity associated with needlefall in the small-block transect may reduce decomposer activity in these soils. Tests of decomposition of standard cellulose material in soils of differing textural and chemical properties indicate decomposition tends to decrease with lower pH and lower levels of nutrients such as potassium (K) and calcium (Ca) (Latter & Harrison 1988). However, note that Brown & Howson (1988) found decomposition rates greater under pine (predominant on the small-block transect) than oak (predominant on the pine barrens transect) due to differences in macroinvertebrate populations and fine-root morphology of these stand types. Initial examination of soil pH from patches typical of the SB versus those of the PB transect indicated that acidity was higher in the A horizon of conifer patch types characteristic of the small-block and hardwood stands had higher A horizon carbon content (Brosofske et al. 2001). These differences may have influenced patch differences in decomposition rates at the 1 cm depth but there were no significant differences in acidity for depths closer to the 4 cm depth. The diversity of overstory cover will also influence C:N ratios and thus the rate of decomposition. Recent modeling work by Fan et al. (1998) indicated that litter quality is a predominant factor determining N mineralization even at the regional extent. Although we standardized the chemical content of our decomposing material, the presence of particular soil fauna associated with mixed litter systems may be an important determinant of decomposition rates (Sulkava & Huhta 1998). Thus, the spatial pattern and dominant scales of decomposition may still be more consistent with the litter quality (e.g., Elliott et al. 1993), which is indirectly determined primarily through manipulation of overstory cover and species (i.e., management prescriptions). Note that the microclimate (CV_2, Fig. 3) and overstory gradients ordered the management patches uniquely, suggesting that overstory influences decomposition independently from its effect on the microclimatic environment.

We expected dominant scales (both resolutions and extents) of decomposition patterns to relate to microclimatic, structural, or vegetative differences among management patches or to the scale of management activities in general. At the transect extent, we further anticipated that the strongest correlations between wavelet transforms of decomposition and our microclimatic, structural, and vegetative variables would occur at resolutions that were dominant in the patterns of decomposition, reflecting those variables most affected by management activities at those resolutions. However, dominant resolutions within decomposition patterns did not appear related to the extent of management patches (average size = 219 m, SB; 310 m, PB). Further, the resolutions of analysis that produced the strongest correlation between overstory – which management activities primarily manipulate- and decomposition were broader than the average size of management patches i.e., 750 m (1 cm depth) and 330 m (4 cm depth) on SB; 490 and 160 m (1 cm depth) and 370 m (4 cm depth), PB). The closest correspondance between average management patch size and overstory was at the 4 cm depth for both transects. Spatial correspondance may be low between functional and other structural, microclimatic or vegetative features due to the highly fragmented nature of these systems, which exist as a mosaic of small, interior habitats with relatively large edge zones. Frequently, structural edges or ecotones apparent at the land surface do not parallel subterranean processes as disturbances can alter overlying vegetation without affecting subsurface, edaphic characteristics (Johnston et al. 1992). Further, ecotones are temporally dynamic and influenced by management in one or more adjacent areas [e.g., Saunders et al. (1999)], reducing the predictability of processes such as decomposition at a fine spatial scale. In addition, factors other than management prescriptions overstory (and correlates) still affect decomposition patterns within these landscapes at some resolutions. For example, measures of topography were correlates of decomposition across the PB transect at 100 m resolution for the 1 cm depth and at broader resolutions of 160–450 m at the 4 cm depth, where associations were stronger. In contrast, topography was a more important correlate with decomposition at the surface along the SB transect, again at relatively broad resolutions. Topography is closely associated with forest productivity and can also influence below-ground nutrient capital (Pregitzer et al. 1983), and could thus be expected to be a primary determinant of decomposition. Topography may also have had an indirect influence on decomposition through its relationship with overstory structure and species composition, and effects on movement of fire, the dominant disturbance regime in the pine barrens. Thus, overstory manipulation may play a relatively greater role at the greater depths and at relatively fine resolutions compared to structural factors, i.e. topography.

We observed some consistencies between transects in variables that were correlated with decomposition. There were also consistent changes in sign of associations with depth between transects. This suggests that some decomposition – structure relationships may transcend management influences and be inherent to the landscape or process being studied. However, the relative importance of the correlates of decomposition differed by depth and by resolution of analysis for both transects at the transect extent. No correlates showed consistent relationships across all resolutions examined (see also Chen et al. 1999). For some transect – depth combinations, correlations with a single variable, e.g., PB 1 cm decomposition with duff depth, showed two distinct peaks of differing sign and magnitude. We suggest that predictive models of functional heterogeneity

should be applied on both a site and scale-specific basis. Inherent scales of process-structure relationships and those imposed by management are confounded within these landscapes. Dominant resolutions of decomposition show limited relationships to resolutions of association with other structural, microclimatic, or vegetative features. There are no apparent characteristic scales of functional heterogeneity to suggest appropriate scales of management. Thus, managers should consider which levels and resolutions of structure-process integrity are important for maintaining long-term resource extraction or specific conservation objectives. Further experimental studies, particularly of different temporal duration, are required to provide mechanistic data on the dynamic of structural-functional relationships across scales. Although our research suggests that these interactions occur at multiple scales, similar work across different geographic regions will determine the generality of these conclusions for theories of pattern-process relationships.

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References

Albert DA (1995) Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. USDA Forest Service, North Central Forest Experiment Station GTR NC-178.

Anderson JM (1992) Responses of soils to climate change. Advances in Ecological Research 22: 163–210.

Austin AT, Vitousek PM (2000) Precipitation, decomposition and litter decomposability of *Metrosideros polymorpha* in native forests on Hawai'i. Journal of Ecology 88: 129–138.

Berg B (1986) Nutrient release from litter and humus in coniferous forest soils – a mini review. Scandinavian Journal of Forest Research 1: 359–369.

Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Calvo de Anta R, Couteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Malkonen E, McClaugherty C, Meentemeyer V, Munox F, Piussi P, Remacle J, Virzo de Santo A (1993) Litter mass loss rates in pine forests of Europe and eastern United States: some relationships with climate and litter quality. Biogeochemistry 20: 127–159.

Berg B, Jansson P-E, Meentemeyer V (1984) Litter decomposition and climate-regional and local models. In: Agren GI (ed) State and change of forest ecosystems-indicators in current research. Department of Ecological and Environmental Research, Swedish University of Agricultural Research, Uppsala (Report 13) pp 389–404.

Binkley D (1984) Does forest removal increase rates of decomposition and nitrogen release? Forest Ecology and Management 8: 229–233.

Bradshaw GA (1991) Hierarchical analysis of pattern and processes of Douglas-fir forests. (PhD Dissertation) Oregon State University, Corvallis, Oregon.

Bradshaw GA, Spies TA (1992) Characterizing canopy gap structure in forests using wavelet analysis. Journal of Ecology 80: 205–215.

Brosofske KD, Chen J, Crow TR (2001) Understory vegetation and site factors: implications for a managed Wisconsin landscape. Forest Ecology and Management. In Press.

Brosofske KD, Chen J, Crow TR, Saunders SC (1999) Vegetation responses to landscape structure at multiple scales across a Northern Wisconsin, USA, pine barrens landscape. Plant Ecology 143: 203–218.

Brown AHF, Howson G (1988) Changes in tensile strength loss of cotton strips with season and soil depth under four tree species. In: Harrison AF, Latter PM, Walton DWH (eds) Cotton strip assay: an index of decomposition in soils. (ITE Symposium No. 24) Institute of Terrestrial Ecology, Grange-over-Sands, England pp 86–89.

Carlile DW, Skalski JR, Batker JE, Thomas JM, Cullinan VI (1989) Determination of ecological scale. Landscape Ecology 2: 203–213.

Chen J, Saunders SC, Crow TR, Naiman RJ, Brosofske KD, Mroz GD, Brookshire BL, Franklin JF (1999) Microclimate in forest ecosystem and landscape ecology. Bioscience 49: 288–297.

Chequamegon National Forest (CNF), Washburn Ranger District (1993) Landscape level analysis, desired future vegetative condition. USDA Forest Service, Park Falls, Wisconsin.

Cuevas E, Medina E (1986) Nutrient dynamics within Amazonian forest ecosystems. I. Nutrient flux in fine litterfall and efficiency of nutrient utilization. Oecologia 68: 466–472.

Dale MRT, Mah M (1998) The use of wavelets for spatial pattern analysis in ecology. Journal of Vegetation Science 9: 805–814.

Dutilleul P, Legendre P (1993) Spatial heterogeneity against heteroscedasticity: an ecological paradigm versus a statistical concept. Oikos 66: 152–171.

Elliott WM, Elliott NB, Wyman RL (1993) Relative effects of litter and forest type on rate of decomposition. American Midland Naturalist 129: 87–95.

Escher N, Käch B, Nentwig W (2000) Decomposition of transgenic *Bacillus thuringiensis* maize by microorganisms and woodlice *Porcellio scaber* (Crutacea: Isopoda). Basic and Applied Ecology 1: 161–169.

Fan W, Randolph JC, Ehman JL (1998) Regional estimation of nitrogen mineralization in forest ecosystems using geographic information systems. Ecological Applications 8: 734–747.

Fogel R, Cromack K Jr (1977) Effects of habitat and substrate quality on Douglas-fir litter decomposition in western Oregon. Canadian Journal of Botany 55: 1632–1640.

Frantzen J, van den Bosch F (2000) Spread of organisms: can traveling and dispersive waves be distinguished? Basic and Applied Ecology 1: 83–91.

French DD (1988) Seasonal patterns in cotton strip decomposition in soils. In: Harrison AF, Latter PM, Walton

DWH (eds) Cotton strip assay: an index of decomposition in soils. (ITE Symposium No. 24) Institute of Terrestrial Ecology, Grange-over-Sands, England, pp 46–49.
Graps A (1995) An introduction to wavelets. Computer Science and Engineering 2: 50–61.
Gray AN, Spies TA (1995) Water content measurement in forest soils and decayed wood using time domain reflectometry. Canadian Journal of Forest Research 25: 376–385.
Heinselman ML (1981) Fire and succession in the conifer forests of northern North America. In: West DC, Shugart HH, Botkin DB. Forest succession: concepts and applications. Springer-Verlag, New York, pp 374–405.
Holling CS (1992) Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62: 447–502.
Johnston CA, Pastor J. Pinay G (1992) Quantitative methods for studying landscape boundaries. In: Hansen A, di Castri F (eds) Landscape boundaries: consequences for biotic diversity. Springer-Verlag, New York, pp 107–125.
Jordan CF (1982) The nutrient balance of an Amazonian rain forest. Ecology 63: 647–654.
Keenan RJ, Kimmins JP (1993) The ecological effects of clearcutting. Environmental Reviews 1: 121–144.
Kirmse RD, Provenza FD, Malecheck JC (1987) Effects of clearcutting on litter production and decomposition in semi-arid tropics of Brazil. Forest Ecology and Management 22: 205–217.
Kochy M, Wilson SD (1997) Litter decomposition and nitrogen dynamics in aspen forest and mixed-grass prairie. Ecology 78: 732–739.
Kurka, A-M, Starr M, Heikinheimo M, Salkinoja-Salonen M (2000) Decomposition of cellulose strips in relation to climate, litterfall nitrogen, phosphorus, and C/N ratio in natural boreal forests. Plant and Soil 219: 91–101.
Latter PM, Harrison AF (1988) Decomposition of cellulose in relation to soil properties and plant growth. In: Harrison AF, Latter PM, Walton DWH (eds) Cotton strip assay: an index of decomposition in soils. (ITE Symposium No. 24) Institute of Terrestrial Ecology, Grange-over-Sands, England, pp 68–71.
Latter PM, Howson G (1977) The use of cotton strips to indicate cellulose decomposition in the field. Pedobiologia B 17: 145–155.
Latter PM, Howson G, Howard DM, Scott WA (1998) Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113: 94–103.
Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943–1967.
Li B-L, Loehle C (1995) Wavelet analysis of multiscale permeabilities in the subsurface. Geophysical Research Letters 22: 3123–3126.
Meentemeyer V (1978) Macroclimate and lignin control of litter decomposition rates. Ecology 59: 465–472.
Meentemeyer V (1984) The geography of decomposition rates. Annals of the Association of American Geographers 74: 551–560.
Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621–626.
Mudrick DA, Hoosein M, Hicks RR Jr, Townsend EC (1994) Decomposition of leaf litter in an Appalachian forest: effects of leaf species, aspect, slope position and time. Forest Ecology and Management 68: 231–250.
Nys C, Howson G (1988) Effects of tree species on forest soils in northern France, detected by cotton strip assay. In: Harrison AF, Latter PM, Walton DWH (eds) Cotton strip assay: an index of decomposition in soils. (ITE Symposium No. 24) Institute of Terrestrial Ecology, Grange-over-Sands, England, pp 90–93.
Oades JM (1988). The retention of organic matter in soils. Biogeochemistry 5: 35–70.
Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44: 322–331.
Prescott CE (1997) Effects of clearcutting and alternative silvlicultural systems on rates of decomposition and nitrogen mineralization in a coastal montane coniferous forest. Forest Ecology and Management 95: 253–260.
Pregitzer KS, Barnes BV, Lemme GD (1983). Relationship of topography to soils and vegetation in an Upper Michigan Ecosystem. Soil Science Society of America J 47: 117–123.
Sagar BF (1988) The Shirley soil burial test fabric and tensile testing as a measure of biological breakdown of textiles. Cotton strip assay: an index of decomposition in soils. In: Harrison AF, Latter PM, Walton DWH (eds) Cotton strip assay: an index of decomposition in soils. (ITE Symposium No. 24) Institute of Terrestrial Ecology, Grange-over-Sands, pp 11–16.
SAS Insitute (1990) SAS user's guide (Version 6). SAS Institute, Cary, North Carolina.
Saunders SC, Chen J, Crow TR, Brosofske KD (1998) Hierarchical relationships between landscape structure and temperature in a managed forest landscape. Landscape Ecology 13: 381–395.
Saunders SC, Chen J, Drummer TD, Crow TR (1999). Modeling temperature gradients across edges over time in a managed landscape. Forest Ecology and Management 117: 17–31.
Stage AR (1976) An expression for the effect of aspect, slope, and habitat type on tree growth. Forest Science 22: 457–460.
Sulkava P, Huhta V (1998) Habitat patchiness affects decomposition and faunal diversity: a microcosm experiment. Oecologia 116: 390–396.
Taylor BR, Parkinson D, Parsons WFJ (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70: 97–104.
Turner M G (1989) Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20: 171–197.
Upadhyay VP, Singh J, Meentemeyer V (1989) Dynamics and weight loss of leaf litter in central Himalayan forests: abiotic versus litter quality influences. Journal of Ecology 77: 147–161.
Van Cleve K, Oliver LK, Schleutner R, Viereck LA, Dyrness CT (1983) Productivity and nutrient cycling in taiga forest ecosystems. Canadian Journal of Forest Research 13: 747–766.
Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. American Naturalist 119: 553–572.
Vitousek PM, Turner DR, Parton WJ, Sanford RL (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawai'i: patterns, mechanisms, and models. Ecology 75: 418–429.
Waring RH, Running AW (1998) Forest ecosystems: analysis at multiple scales. Academic Press, San Diego, CA.
Wiens JA (1989) Spatial scaling in ecology. Functional Ecology 3: 385–397.