



Research article

Empirical patterns of the effects of changing scale on landscape metrics

Jianguo Wu^{1,*}, Weijun Shen², Weizhong Sun³ and Paul T. Tueller⁴

¹Department of Plant Biology, Arizona State University, Tempe, AZ 85287-1601, USA; ²Chinese Academy of Sciences, South China Institute of Botany, Guangzhou, 510650, P. R. China; ³Water Services Department, City of Phoenix, Phoenix, AZ 85003, USA; ⁴Department of Environmental and Resource Sciences, University of Nevada, Reno, NV 89512, USA; *Author for correspondence (e-mail: Jingle.Wu@asu.edu)

Received 11 September 2001; accepted in revised form 30 October 2002

Key words: Anisotropy, Extent, Grain, Landscape metric scalograms, Landscape pattern analysis, Scale effect

Abstract

While ecologists are well aware that spatial heterogeneity is scale-dependent, a general understanding of scaling relationships of spatial pattern is still lacking. One way to improve this understanding is to systematically examine how pattern indices change with scale in real landscapes of different kinds. This study, therefore, was designed to investigate how a suite of commonly used landscape metrics respond to changing grain size, extent, and the direction of analysis (or sampling) using several different landscapes in North America. Our results showed that the responses of the 19 landscape metrics fell into three general categories: Type I metrics showed predictable responses with changing scale, and their scaling relations could be represented by simple scaling equations (linear, power-law, or logarithmic functions); Type II metrics exhibited staircase-like responses that were less predictable; and Type III metrics behaved erratically in response to changing scale, suggesting no consistent scaling relations. In general, the effect of changing grain size was more predictable than that of changing extent. Type I metrics represent those landscape features that can be readily and accurately extrapolated or interpolated across spatial scales, whereas Type II and III metrics represent those that require more explicit consideration of idiosyncratic details for successful scaling. To adequately quantify spatial heterogeneity, the metric-scalograms (the response curves of metrics to changing scale), instead of single-scale measures, seem necessary.

Introduction

An ultimate goal of studying spatial pattern in ecology is to understand its interactions with ecological processes (Turner 1989; Levin 1992; Wu and Levin 1994). To relate pattern to process, we often have to quantify spatial heterogeneity explicitly at multiple scales as a first step. Unfortunately, our knowledge is still rather limited about the scale-dependence of pattern metrics and the general scaling relationships of landscape pattern. It has been widely recognized that spatial pattern is scale-dependent; that is, it changes with the scale of observation or analysis (e.g., Gardner et al. (1987) and Meentemeyer and Box (1987), Woodcock and Strahler (1987), Turner et al. (1989),

O'Neill et al. (1991, 1996), He and Legendre (1994), Moody and Woodcock (1995), Jelinski and Wu (1996), Qi and Wu (1996), Gardner (1998), Wu et al. (2000)). Numerous recent studies, reporting various scale effects, have shed light on the problem of scale in pattern analysis, but most of these studies examined only a few metrics or covered only a narrow range of scales. Thus, although we are well aware that changing grain size or extent often affects landscape metrics, it is not clear if these effects exhibit any general patterns (or scaling relations) consistent across real landscapes.

Apparently, variables that characterize landscape pattern, such as the number, area, and spatial pattern of different patch types, will change when scale (grain

size and/or extent) is altered (Wiens 1989; Wu 1999). One may argue that the 'scale effect' is caused not only by changing grain size or extent itself, but also by associated changes in landscape composition (e.g., diversity of patch types) and configuration (e.g., spatial arrangement of different patch types). This problem is somewhat similar to the 'area effect' of island biogeography (MacArthur and Wilson 1967; Wu and Vankat 1991, 1995), where increasing area is usually accompanied with a suite of changing abiotic and biotic factors. To understand effects of increased habitat area (allowing for larger population sizes and thus lower species extinction probabilities) versus effects due to increased habitat heterogeneity (corresponding to more available niches) on the dynamics of species richness, one must separate 'pure' versus 'total', area effect (Buckley 1985; Williamson 1988). Similarly, to understand the 'pure' scale effect in landscape pattern analysis one must hold all other variables constant as grain size or extent is varied (e.g., Saura and Martinez-Millan (2001)). Also, one may want to know how pattern metrics change with scale for landscapes with known and systematically varying properties (e.g., the number of patch types and their abundance and spatial pattern). This would require simulated or artificial landscape data, which are usually generated from a priori knowledge of what the pattern is (e.g., auto-correlated spatial patterns with varying proportions of different patch types from fractal or stochastic simulation algorithms). This paper first describes these patterns using empirical landscape data, allowing artificial landscape to be analyzed at a later stage.

The goal of this study was to systematically investigate how commonly used landscape metrics respond to changing grain size and extent (as well as the direction of analysis or sampling) with several considerably different landscapes in North America. In addition, we attempted to explore the generalities and idiosyncrasies in the response of landscape metrics to changing scale, and to derive scaling relations based on an inductive, empirical approach. To achieve this goal, we conducted a series of analyses to address the following questions: (1) How does changing grain size affect the results of landscape metrics? (2) How does changing extent and the direction of analysis affect the results of different landscape metrics? (3) How do various landscape metrics differ in their response to changing scale? (4) What are the scaling relations for different pattern metrics, and how robust are they across different landscapes?

Data and methods

To capture the diversity of landscape patterns, we used land use and land cover maps of five landscapes with contrasting natural and socioeconomic settings: a boreal forest landscape (near Thompson, Manitoba, Canada, 55°45' N, 98°30' W) with minimal human influences, two Great Basin landscapes (within the state of Nevada, USA; Minden: 38°48' N, 119°30' W, Washoe: 39°06' N, 119°50' W) with moderate human modifications, and two urban landscapes in the Phoenix, Arizona, USA metropolitan area (33°18' N, 112°02' W) representing a region profoundly modified by human activities (Figure 1). Land use and land cover types of each study site are listed in Table 1. The spatial resolution for all data sets was 30 × 30 m, and the extent was 357 km² (630 × 630 pixels) for the boreal forest landscape (Boreal hereafter), 900 km² (1000 × 1000 pixels) for the Minden landscape, Carson City, Nevada, USA (Minden hereafter), 380 km² (650 × 650 pixels) for the Washoe valley landscape, Washoe County, Nevada, USA (Washoe hereafter), and 2025 km² (1500 × 1500 pixels) and 3600 km² (2000 × 2000 pixels) for the two Phoenix landscapes (Phx_1 and Phx_2 hereafter).

The vegetation map of the boreal forest landscape in Manitoba, Canada, derived from a Landsat TM scene of August 1988, was obtained from the BOREAS project's web site (http://boreas.gsfc.nasa.gov/BOREAS/images/NSA_class.gif). The downloaded JPEG file was then converted into the raster format using ArcView and Spatial Analyst. The boreal forest landscape was composed of 11 patch types, including various coniferous and deciduous forest stands, regenerated forest stands of different age, fen communities, water bodies, and burned areas. It exhibited a high degree of spatial heterogeneity induced and maintained by a variety of natural processes. The dominant tree species include: black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), white birch (*Betula papyrifera*), and trembling aspen (trembling aspen).

The two Great Basin data sets were classified vegetation maps based on 1984 Landsat TM scenes for the Minden area and Washoe Valley of Nevada in the western Great Basin, respectively. Both of these two landscapes contained different types of arid plant communities (primarily shrublands and woodlands) and burned areas. Dominant plant species in shrublands included sagebrush (*Artemisia spp.*), and salt desert shrub (*Sarcobatus spp.*), whereas those in

woodlands included pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*). With Carson City spreading out and agricultural fields scattering around, the Minden landscape was more conspicuously transformed by human activities than the Washoe landscape whose natural vegetation was much less disturbed. It was also obvious from visualizing the land use and land cover map that the Minden landscape was composed of several somewhat north–south oriented vegetation (or land cover) zones.

Phoenix is located in the northern part of the Sonoran desert in the State of Arizona, and is the home of the Central Arizona-Phoenix Long-Term Ecological Research (CAPLTER) Project, one of the two new urban LTER sites supported by the US National Science Foundation. Native vegetation is characterized by desert scrub communities dominated by creosote bush (*Larrea tridentata*), mesquite (*Prosopis glandulosa*), and several other shrub species, including the magnificent cactus, saguaro (*Carnegiea gigantea*) – the most recognized symbol of the Sonoran desert landscape. In the past several decades this region has experienced tremendous land transformation as Phoenix has become the fastest growing city in the United States. As a consequence of the rapid urbanization, the composition and spatial structure of the Phoenix landscape have changed dramatically (Jenerette and Wu 2002; Luck and Wu 2002). The Phoenix urban landscape data were obtained by rasterizing the vector-based 1995 land use map (originally produced by the Maricopa Association of Governments) at the 30-meter resolution. To examine the sensitivity of landscape metrics to shifting geographic locations of the study area within the same region, we clipped two study landscapes from the Phoenix area (see Figure 1D): Phx_1 (1500 × 1500 pixels in size and centering at the urban core area) and Phx_2 (1500 × 1500 pixels in size and covering the transitional zone from the Sonoran desert north of Phoenix to the city itself).

To investigate the effects of changing grain size, four data sets (Boreal, Minden, Phx_1 and Phx_2) were used. When the extent was kept the same as the original data sets, the grain size was systematically changed from 1 by 1 to 100 by 100 pixels for all four landscapes (Figure 2, Table 2), following the majority rule. That is, a new aggregated areal unit was assigned to the patch type that was the most dominant among those represented by all pixels at the next lower level. When two or more patch types were tied, a random selection was allowed (Figure 3). Note that in this study the aggregation at each successive grain

size always started with the original (1 × 1 pixel) data. This may be called the ‘independent’ aggregation scheme as opposed to the ‘iterative’ aggregation scheme in which the aggregation at the next grain size is based on the already-aggregated data of the initial grain size (see Turner et al. (1989); R. H. Gardner, pers. comm.).

To investigate the effects of changing extent, we systematically varied the size of the map while keeping grain size constant. In particular, we increased the extent from 50 to 630 pixels on a side (i.e. 2.25 to 357 km²) for Boreal, from 50 to 1000 pixels on a side (i.e. 2.25 to 900 km²) for Minden, from 100 to 650 pixels on a side (i.e. 9 to 380 km²) for Washoe, from 300 to 1500 pixels on a side (i.e. 81 to 2025 km²) for Phx_1, and from 300 to 2000 pixels on a side (i.e. 81 to 3600 km²) for Phx_2 (see Table 2 for details of the increments). Because landscape pattern is rarely isotropic, we also investigated how the direction of analysis might affect the changing extent analysis. To do this, we repeated the analysis with varying extents in four diagonal directions for each of three data sets: Minden, Washoe, and Phx_1 (Figure 2, Table 2). For Minden and Washoe, the values of the indices for the four directions converged as the same largest extent was reached. In the case of Phx_1, the four directions did not converge to the same largest extent because the original grid was of a rectangular shape (1500 by 2447 pixels; see Figure 1D).

We examined 19 landscape metrics (Table 3). The landscape pattern analysis package, FRAGSTATS (McGarigal and Marks 1995), was used to compute 18 of the 19 metrics. Square pixel (see definition in Table 3; Frohn (1998)) was added to the package by modifying the C code of FRAGSTATS 2.0. In total, these metrics were examined at 331 single scales for the five landscape data sets (235 for changing extent and 96 for changing grain size; see details in Table 2).

Results

The results are presented in two sections: effects of changing grain size (Figure 4), and effects of changing extent and the direction of analysis (Figures 5 and 6). In each section, results of different landscapes are given in the order of Boreal, Minden, Washoe, Phx_1, and Phx_2. For each landscape, we summarized the results of the 19 metrics in the form of ‘landscape metric scalograms’ in which pattern indices were plotted against grain size or extent. Due to space lim-

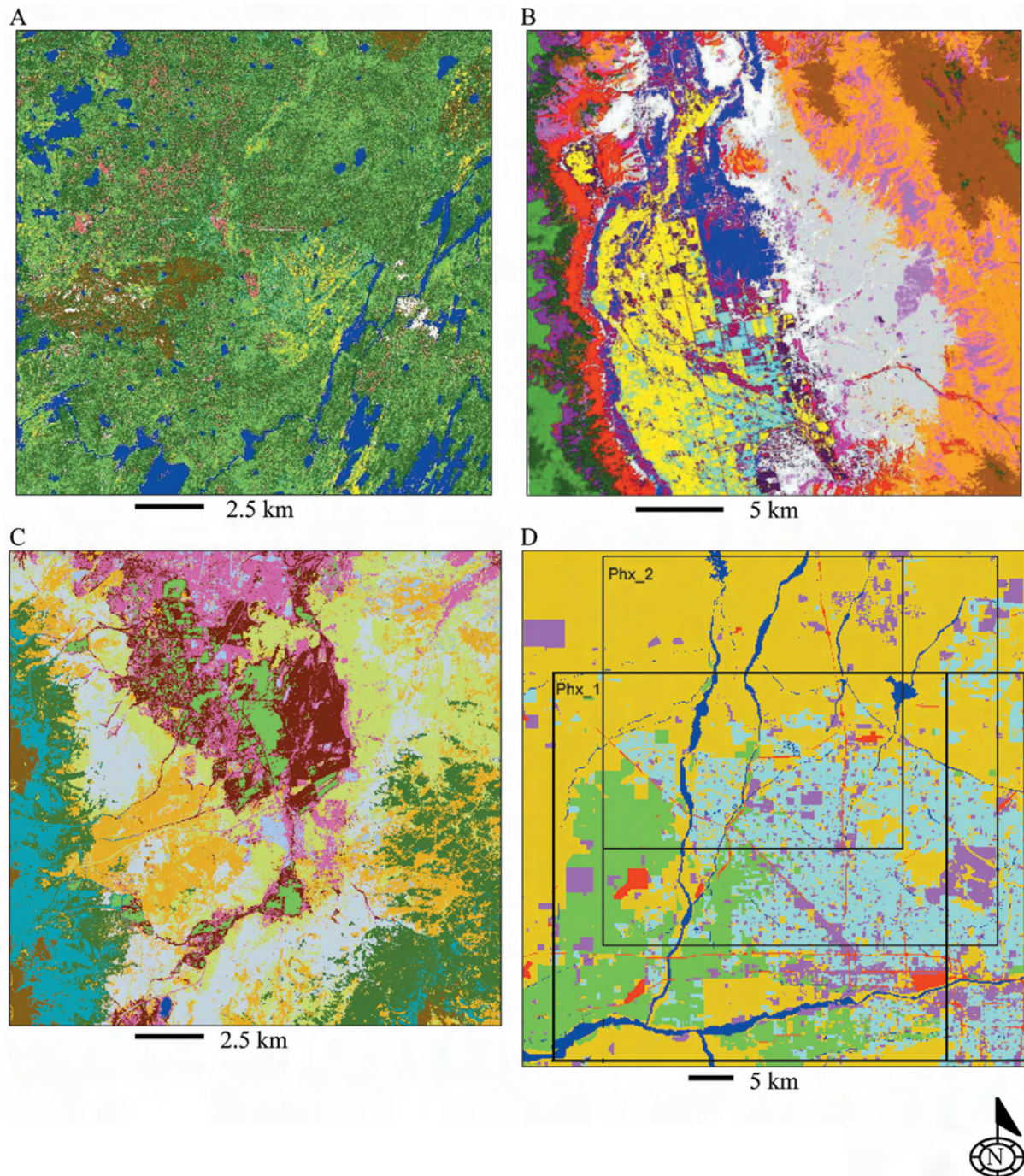


Figure 1. Maps of the different landscapes used for the study: (A) A boreal forest landscape in Manitoba, Canada, with 11 patch types including various forest stands, disturbed areas and water; (B) Minden landscape in the Great Basin, Nevada, USA, with 15 patch types including native arid plant communities, burned areas, and urban and agricultural land uses; (C) Washoe valley landscape in the Great Basin, Nevada, USA, with 11 patch types most of which were shrublands; (D) The metropolitan Phoenix landscape (Arizona, USA) with 24 patch types that were dominated by various urban and agricultural land uses. Two data sets were extracted: Phx_1 (thick line) covered much of the central Phoenix area, whereas Phx_2 (thin line) was a desert-to-urban transitional landscape. In each data set, the inner boundary denotes the area used for changing grain size analysis, and the outer boundary for changing extent analysis. See Table 1 for a complete list of all the specific patch types.

Table 1. Land use and land cover types in the study landscapes (see Figure 1 for the corresponding maps).

Boreal (357.2 km ²)	Minden (380.3 km ²)	Washoe (900 km ²)	Phoenix (Phx_1: 2025 km ² , Phx_2: 3600 km ²)
Land use and Land Cover Types			
Wet conifer	Water	Water	Rural
Dry conifer	Mixed conifer	Eastside pine (Jeffrey pine dominated forest)	Large lot residential
Mixed forest	Chaparral	Chaparral	Small lot residential
Deciduous forest stand	Pinyon-Juniper woodland	Pinyon-Juniper woodland	Medium density residential
Fen	Greasewood	Big sagebrush and bitterbrush shrublands	High density residential
Water	Bitter sage	Big sagebrush shrubland	Neighborhood retail center
Disturbed site	Sparse vegetation	Sparse vegetation	Community retail center
Regenerated young forest	Fallow agricultural field	Fallow crop field or dry riparian area	Regional retail center
Regenerated medium forest	Burned area	Burned area or low seral community	Hotel, motel or resort
Regenerated older forest	Agriculture (Alfalfa)	Irrigated agriculture and wet riparian area	Warehouse or Distribution Center
Burned area	Urban area	Urban area	Industrial
	Sagebrush		Business Park
	Low Sagebrush		Office
	Meadow/pasture		Educational
	Riparian		Institutional
			Public facility
			Large assembly area
			Transportation
			Airport
			Recreational open space
			Dedicated or non-developable open space
			Water
			Agriculture
			Vacant

itation, we were only able to show a few landscape metrics in the form of scalograms representing different types of general scaling relations.

Effects of changing grain size

In general, changing grain size had significant effects on the values of landscape metrics. Although the magnitude and pattern of these responses varied among metrics and across landscapes, the effects of changing grain size can be grouped into three general types: Type I – predictable responses with simple scaling relations; Type II – staircase-like responses with no simple scaling relations; and Type III – er-

atic responses exhibiting no general scaling relations (Table 4).

Twelve of the nineteen landscape metrics we examined belonged to Type I, including the number of patches (NP), patch density (PD), total edge (TE), edge density (ED), landscape shape index (LSI), area-weighted mean shape index (AWMSI), area-weighted mean patch fractal dimension (AWMFD), patch size coefficient of variation (PSCV), mean patch size (MPS), square pixel index (SqP), patch size standard deviation (PSSD), and largest patch index (LPI). These metrics changed predictably with increasing grain size, exhibiting simple scaling relationships that were robust across the different landscapes (Figure 4, Table 4). Eight metrics decreased in their values with

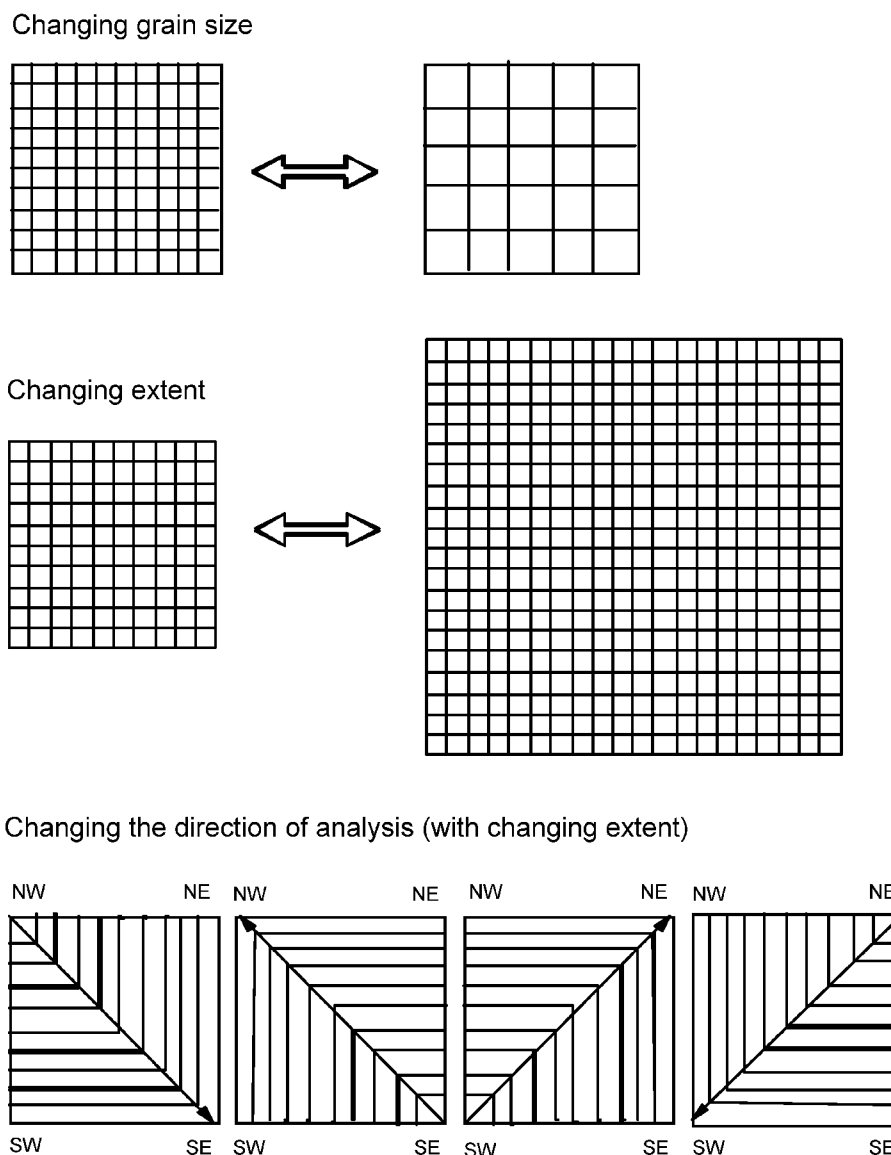


Figure 2. A schematic representation of three different ways of altering the scale of analysis in this study: changing extent, changing grain size, and changing the direction of analysis with increasing extent.

increasing grain size with a power-law relationship. Although these response curves could also be fit with an exponential decay function, the regression coefficient (R^2) was usually lower. Considering that the four landscapes (Boreal, Minden, Washoe, and Phx_2) were quite different in both patch composition and spatial configuration, the consistency of the power-law relationship among them was remarkable. However, the values of the parameters in the scaling relation changed considerably among different landscapes, indicating their structural differences at dis-

tinctive grain sizes. SqP, a normalized perimeter-area ratio, decreased linearly with increasing grain size. PSSD, MPS, and LPI all increased with grain size consistently among different landscapes.

In contrast with Type I, the Type II metrics (PR, PRD and SHDI) decreased in a staircase-like fashion with increasing grain size across different landscapes (Figure 4 and Table 4). The total number and height of the steps did not appear predictable because they were determined inherently by the idiosyncratic structural details of the specific landscapes. This behav-

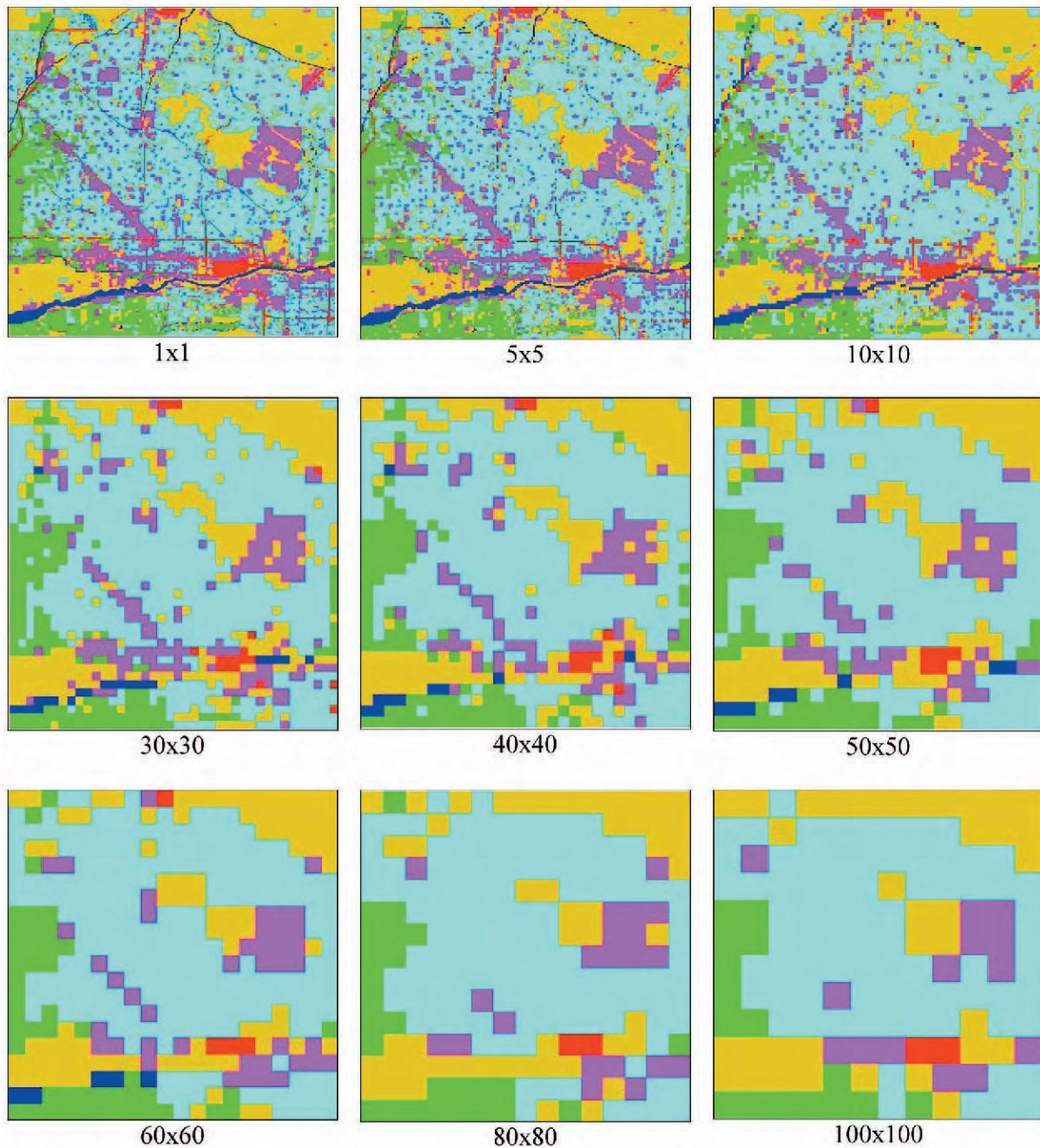


Figure 3. The land use and land cover maps of the central Phoenix urban landscape (Phx_2) with different grain sizes or spatial resolutions, ranging from 1×1 to 100×100 original Landsat TM pixels. At the grain size of 1×1 pixel, the landscape had 24 patch types that were dominated by various urban and agricultural land uses (see Table 1 for more details).

ioral pattern could be readily understood in terms of PR, whose values decreased intermittently as integers when progressive aggregation of pixels eliminated patch types that had small and scattered patches (Figures 3 and 5). The staircase-like behavior of PRD was

simply reflective of PR, but less pronounced due to the rescaling by the total landscape area. The steps in the response curve of SHDI seemed even less obvious, although still recognizable in most cases, because the relative abundance of patch types also con-

Table 2. List of the grain sizes and extents used in the study of effects of changing scale on landscape metrics for different landscapes. Both grain size and extent are expressed in terms of the number of pixels in the original data set each grain size or extent contains on one side. Three landscapes were used for examining effects of changing directions of analysis.

Changing Grain				Changing Extent				
(The number of pixels on a side)				(The number of pixels on a side)				
Boreal	Minden	Phx_1	Phx_2	Boreal	Minden	Washoe	Phx_1	Phx_2
1	1	1	1	50	50	100	300	300
2	2	2	2	70	100	150	400	350
3	3	3	3	90	150	200	500	400
4	4	4	4	100	200	250	600	450
5	5	5	5	110	250	300	700	500
6	6	6	6	130	300	350	800	600
7	7	7	7	150	350	400	900	700
8	8	8	8	170	400	450	1000	800
9	9	9	9	190	450	500	1100	900
10	10	10	10	200	500	550	1200	1000
11	11	11	11	210	550	600	1300	1100
12	12	12	12	230	600	650	1400	1200
13	13	13	13	250	650		1500	1300
14	14	14	14	270	700			1400
15	15	15	15	290	750			1500
20	20	20	20	300	800			1600
30	30	30	30	310	850			1700
40	40	40	40	330	900			1800
50	50	50	50	350	950			1900
60	60	60	60	370	1000			2000
70	70	70	70	390				
80	80	80	80	400				
90	90	90	90	410				
100	100	100	100	430				
				450				
				470				
				490				
				500				
				510				
				530				
				550				
				570				
				590				
				600				
				630				
24	24	24	24	35	20 X	12 X	13 X	20
					4 directions	4 directions	4 directions	

Total number of single-scale evaluations = 96 + 235 = 331

tributed to the values of SHDI. Nevertheless, the general pattern of SHDI could be approximated, with varying degrees of accuracy, using a decreasing logarithmic function (Table 4).

Type III included 4 metrics: landscape (double-log) fractal dimension (DLFD), contagion (CONT), mean patch fractal dimension (MPFD), and mean patch shape index (MSI). These metrics did not show consistent responses among different landscapes, and

Table 3. List of landscape metrics used in the study. All metrics, except square pixel index, were based on McGarigal and Marks (1995).

Landscape Metric	Abbreviation	Description
Number of Patches	NP	The total number of patches in the landscape.
Patch Density	PD	The number of patches per unit area, e.g., per km ²
Total Edge	TE	The sum of the lengths of all edge segments (unit: m).
Edge Density	ED	The total length of all edge segments per ha for the class or landscape of consideration (unit: m/ha).
Patch Richness	PR	The number of different patch types in the landscape.
Patch Richness Density	PRD	The number of patch types per unit area
Shannon's Diversity Index	SHDI	A measure of patch diversity in a landscape that is determined by both the number of different patch types and the proportional distribution of area among patch types: $H = - \sum_{i=1}^m p_i \ln(p_i)$ where m is the total number of patch types and p_i is the proportion of the landscape area occupied by patch type i (unitless).
Largest Patch Index	LPI	The ratio of the area of the largest patch to the total area of the landscape (unit: %).
Mean Patch Size	MPS	The average area of all patches in the landscape (unit: ha).
Patch Size Standard Deviation	PSSD	The standard deviation of patch size in the entire landscape (unit: ha).
Patch Size Coefficient of Variation	PSCV	The standard deviation of patch size divided by mean patch size for the entire landscape (unit: %).
Landscape Shape Index	LSI	A modified perimeter-area ratio of the form: $LSI = \frac{0.25E}{\sqrt{A}}$ where E is the total length of patch edges and A is the total area of the landscape (unitless).
Mean Patch Shape Index	MSI	A patch-level shape index averaged over all patches in the landscape: $MSI = \frac{\sum_{i=1}^m \sum_{j=1}^n \left[\frac{0.25P_{ij}}{\sqrt{a_{ij}}} \right]}{N}$ where P_{ij} and a_{ij} are the perimeter and area of patch ij , respectively, and N is the total number of patches in the landscape (unitless).
Area-Weighted Mean Patch Shape Index	AWMSI	Mean patch shape index weighted by relative patch size: $AWMSI = \sum_{i=1}^m \sum_{j=1}^n \left[\left(\frac{0.25P_{ij}}{\sqrt{a_{ij}}} \right) \left(\frac{a_{ij}}{A} \right) \right]$ where P_{ij} and a_{ij} are the perimeter and area of patch ij , respectively, A is the total area of the landscape, m is the number of patch types, and n is the total number of patches of type i (unitless).
Double-Log Fractal Dimension	DLLFD	The fractal dimension for the entire landscape which is equal to 2 divided by the slope of the regression line between the logarithm of patch area and the logarithm of patch perimeter: $DLFD = \frac{2}{\left[\frac{N \sum_{i=1}^m \sum_{j=1}^n (\ln(P_{ij}) \ln(a_{ij})) - \left(\sum_{i=1}^m \sum_{j=1}^n \ln(a_{ij}) \right)}{\left(N \sum_{i=1}^m \sum_{j=1}^n (\ln(P_{ij}^2)) - \left(\sum_{i=1}^m \sum_{j=1}^n \ln(P_{ij}) \right)^2 \right)} \right]}$ where P_{ij} and a_{ij} are the perimeter and area of patch ij , respectively, m is the number of patch types, n is the total number of patches of type i , and N is the total number of patches in the landscape (unitless).

Table 3. Continued

Landscape Metric	Abbreviation	Description
Mean Patch Fractal Dimension	MPFD	<p>The average fractal dimension of individual patches in the landscape, which is the summation of fractal dimension for all patches divided by the total number of patches in the landscape:</p> $FD = \frac{\sum_{i=1}^m \sum_{j=1}^n \left(\frac{2\ln(0.25P_{ij})}{\ln(a_{ij})} \right)}{N}$ <p>where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, m is the number of patch types, n is the total number of patches of type i, and N is the total number of patches in the landscape (unitless).</p>
Area-Weighted Mean Patch Fractal Dimension	AWMPFD	<p>The patch fractal dimension weighted by relative patch area:</p> $AWMPFD = \sum_{i=1}^m \sum_{j=1}^n \left(\frac{2\ln(0.25P_{ij})}{\ln(a_{ij})} \left(\frac{a_{ij}}{A} \right) \right)$ <p>where P_{ij} and a_{ij} are the perimeter and area of patch ij, respectively, m is the number of patch types, n is the total number of patches of type i, and A is the total area of the landscape (unitless).</p>
Contagion	CONT	<p>An information theory-based index that measures the extent to which patches are spatially aggregated in the landscape (Li and Reynolds 1993):</p> $CONT = \left[1 + \sum_{i=1}^m \sum_{j=1}^m p_{ij} \ln(p_{ij}) / 2\ln(m) \right] (100)$ <p>where p_{ij} is the probability that two randomly chosen adjacent pixels belong to patch type i and j, m is the total number of patch types in the landscape (unitless).</p>
Square Pixel	SqP	<p>A normalized perimeter-area ratio of the form (Frohn 1998):</p> $SqP = 1 - \frac{4\sqrt{A}}{E}$ <p>where A is the total area of the landscape and E is the total amount of edges (unit: unitless).</p>

the shape of their response curves was sensitive to the specific landscape pattern. In particular, DLFD and CONT exhibited erratic responses to increasing grain size for different landscapes. For the boreal landscape, DLFD changed only slightly at first, but declined rapidly (and linearly) as grain size further increased (Figure 4). While the response curve of DLFD for Minden was similar to that for Boreal, drastically different responses were found for the two Phoenix landscape data sets. In the case of the central Phoenix urban landscape (Phx_1; Figure 3), DLFD increased rapidly and then reached a relatively constant value, whereas in the case of the transitional Phoenix landscape (Phx_2) DLFD increased rapidly, stayed relatively unchanged, and then declined drastically as grain size further increased (Figure 4). In a similarly idiosyncratic manner, CONT increased monotonically for Boreal, increased first and then declined for Minden, and decreased rapidly first and then fluctuated with further increase in grain size for

the two Phoenix landscapes (Figure 4). The response curves of MSI and MPFD resembled each other closely, and both varied among different landscapes. However, as grain size continued to increase, MSI and MPFD tended to become invariant.

Effects of changing extent and direction of analysis

In general, changing extent also had significant and variable effects on the values of landscape metrics. However, similar to the case of changing grain size, the responses of landscape metrics to changing extent could also be grouped into three general types: Type I – Predictable responses with simple scaling relationships; Type II – Staircase-like responses with no simple scaling relationships; and Type III – Erratic responses with no scaling relationships (Table 5).

Type I metrics included NP, TE, SqP, PRD, SHDI, and LSI, which could be described by simple scaling equations of either a linear, power-law, or logarithmic

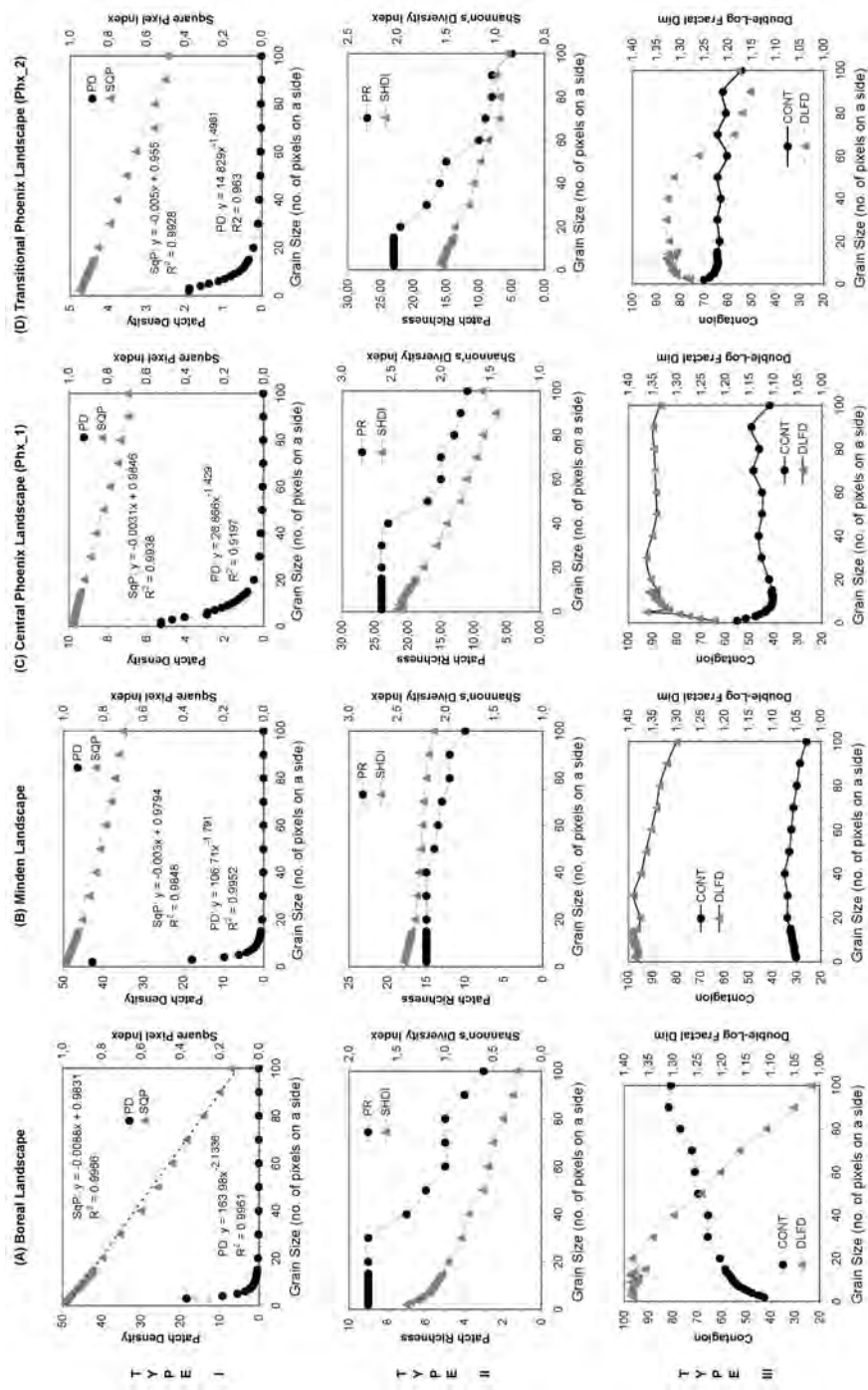


Figure 4. Scalograms showing effects of changing grain size on landscape metrics. The rows are examples of the three types of metrics in terms of their responses to changing grain size, and the columns represent different landscapes: (A) a boreal forest landscape, (B) the Minden landscape in the Great Basin, (C) the central Phoenix urban landscape, and (D) a transitional landscape in the Phoenix region.

Table 4. Scaling relations of landscape metrics with respect to grain size. Subscript g in equations denotes grain size.

Landscape Metric	Scaling Relations and Characteristics
<p>Type I (Grain Size): Metrics showing predictable changes and simple scaling relations.</p> <p>The response curves of these metrics show unique general scaling relationships across landscapes. Therefore, the extrapolation and interpolation of Type I metrics across different grain sizes can be simply and accurately done based on only a few data points.</p>	
Number of Patches	A decreasing power function:
Total Edge	$y_g = \alpha x_g^\beta$, $\alpha > 0$, $\beta < 0$, and $x_g \geq 1$
Patch Density	where y_g is the value of a metric, α and β are constants, and x_g is the grain size.
Edge Density	
Landscape Shape Index	<ul style="list-style-type: none"> The rate of decrease in the metric value varies, but the scaling relationship is rather robust, among disparate landscapes.
Area-Weighted Mean Shape Index	
Area-Weighted Mean Patch Fractal Dimension	<ul style="list-style-type: none"> Although an exponential decay function may also be used here, the power law relationship generally gives a better goodness of fit.
Patch Size Coefficient of Variation	
Mean Patch Size	<p>An increasing power law function:</p> $y_g = \alpha x_g^\beta$ <p>$\alpha > 0$, $\beta > 0$, and $x_g \geq 1$</p> <p>where y_g is the value of a metric, α and β are constants, and x_g is the grain size.</p>
Square Pixel Index	<p>A declining linear function:</p> $y = ax + b$ <p>$a < 0$, $b > 0$, and $x_g \geq 1$</p> <p>where y_g is the value of a metric, a and b are constants, and x_g is the grain size.</p>
Patch Size Standard Deviation	<p>An increasing linear function:</p> $y_g = ax_g + b$ <p>$a > 0$ and $x_g \geq 1$</p> <p>where y_g is the value of a metric, a and b are constants, and x_g is the grain size.</p>
Largest Patch Index	<p>An increasing power law or logarithmic function:</p> $y_g = \alpha x_g^\beta$ <p>$\alpha > 0$, $0 < \beta < 1$, and $x_g \geq 1$ or $y_g = a \log x_g + b$, $a > 0$ and $x_g \geq 1$</p> <p>where y_g is the value of a metric, α, β, a and b are constants, and x_g is the grain size.</p>
<p>Type II (Grain Size): Metrics showing staircase-like responses.</p> <p>These metrics do not follow a simple scaling function, but a staircase-like pattern is found across different landscapes. In contrast with Type I metrics, the values of Type II metrics at different grain sizes can not be accurately predicted based on only a few data points.</p>	
Patch Richness	<ul style="list-style-type: none"> The value of the metric declines in a stepping-down staircase fashion as grain size increases for a given landscape.
Patch Richness Density	<ul style="list-style-type: none"> The number of steps and their height vary erratically among landscapes.
Shannon's Diversity Index	<ul style="list-style-type: none"> The general pattern of SHDI can be approximated with a decreasing logarithmic function: $y_g = a \log x_g + b$ <p>$a < 0$, $b > 0$, and $x_g \geq 1$</p> <p>where y_g is the value of a metric, α, β, a and b are constants, and x_g is the grain size.</p>
<p>Type III (Grain Size): Metrics showing erratic responses.</p> <p>The response curves of these metrics are sensitive to the specific pattern of the landscape, and do not show consistent patterns across different landscapes. As a result, general scaling functions seem impossible to derive. Thus, the extrapolation or interpolation of these metrics must explicitly consider the spatial structure of the landscapes.</p>	
Contagion	<ul style="list-style-type: none"> No consistent scaling relationship among different landscapes.
Landscape Fractal Dimension	<ul style="list-style-type: none"> The response curves may take various forms: no obvious change, monotonic changes, or fluctuations.
Mean Patch Shape Index	
Mean Patch Fractal Dimension	<ul style="list-style-type: none"> MPFD and MSI are relatively insensitive to changing grain size.

function (see Table 5 for details). NP, TE, LSI, and SqP again showed robust, simple scaling relations.

Conceivably, the power function of PRD was simply the result of the arithmetic increase in the number of

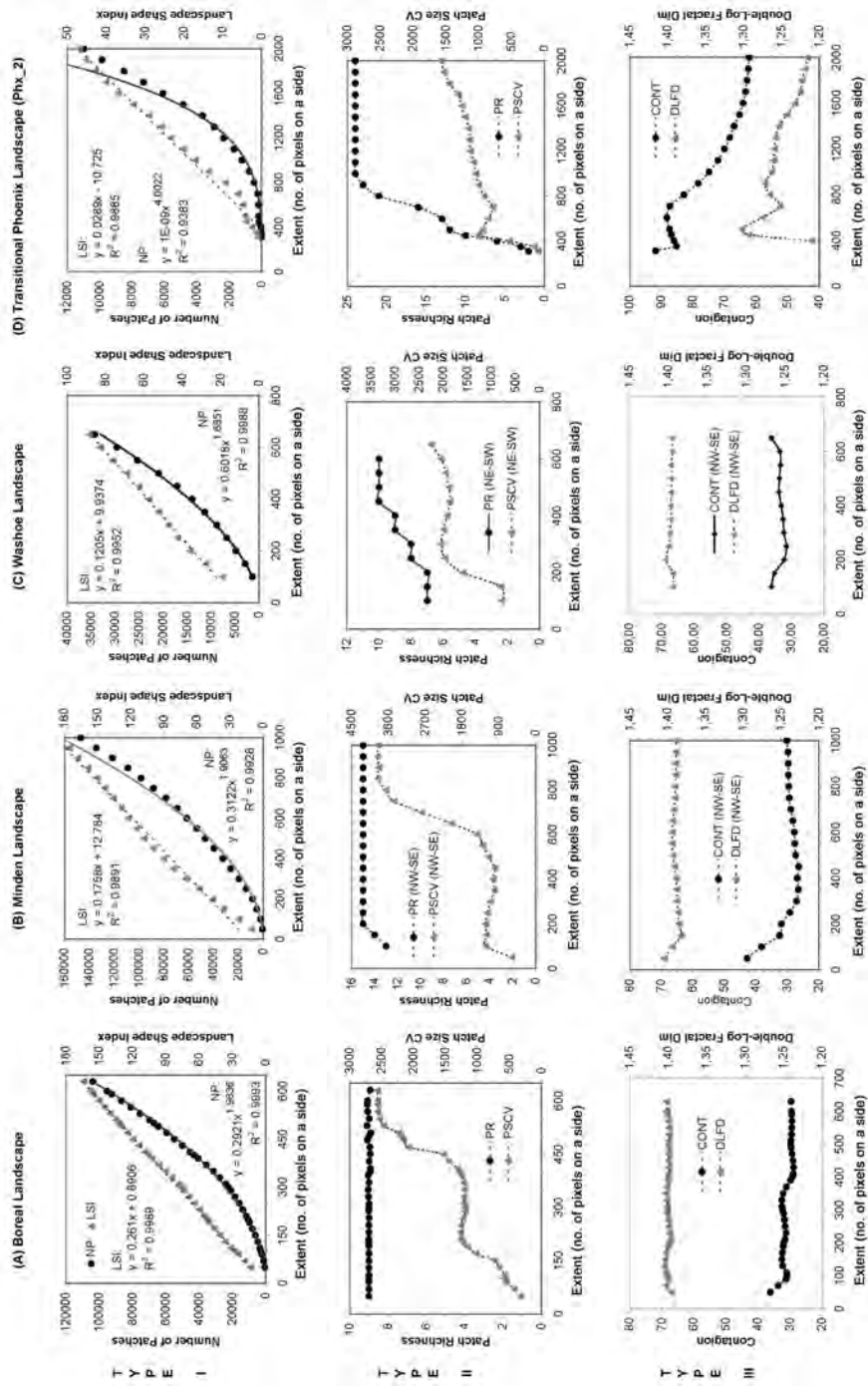


Figure 5. Scalograms showing effects of changing extent on landscape metrics. The rows are examples of the three types of metrics in terms of their responses to changing extent, and the columns represent different landscapes: (A) a boreal forest landscape, (B) the Minden landscape in the Great Basin, (C) the Washoe landscape in the Great Basin, and (D) the transitional landscape in the Phoenix region. For landscapes A and D, extent was increased progressively from northwest to southeast diagonally, while landscapes B and C were analyzed from all four diagonal directions.

Table 5. Scaling relations of landscape metrics with respect to extent. Subscript e in equations denotes extent.

Type I (Extent): Metrics showing predictable changes and simple scaling relations

The response curves of these metrics show consistent, general scaling relationships across landscapes. Therefore, the extrapolation and interpolation of Type I metrics across different extents can be simply and accurately done based on only a few data points.

Landscape Metric	Scaling Relations and Characteristics
Number of Patches	<u>An increasing power law function:</u>
Total Edge	$y_e = \alpha x_e^\beta$, $\alpha > 0$, $\beta > 0$, and $x_e > 1$ where y_e is the value of a metric, α and β are constants, and x_e is the extent.
Square Pixel Index	<u>An increasing power function or a logarithmic function:</u> $y_e = \alpha x_e^\beta$, $\alpha > 0$, $0 < \beta < 0$, and $x_e > 1$ or, $y_e = a \log x_e + b$, $a > 0$, and $x_e > 1$ where y_e is the value of a metric, α , β , a and b are constants, and x_e is the extent.
Shannon's Diversity Index	<u>An increasing logarithmic function:</u> $y_e = a \log x_e + b$, $a > 0$, $x_e > 1$ where y_e is the value of a metric, a and b are constants, and x_e is the extent.
Patch Richness Density	<u>A power law function:</u> $y_e = \alpha x_e^\beta$, $\alpha > 0$, $\beta < 0$, and $x_e > 1$ where y_e is the value of a metric, α and β are constants, and x_e is the extent.
Landscape Shape Index	<u>A linear function:</u> $y_e = a x_e + b$, $a > 0$, $b > 0$, and $x_e > 1$ where y_e is the value of a metric, a and b are constants, and x_e is the extent.

Type II (Extent): Metrics showing staircase-like responses.

The response curves of these metrics do not show unique simple scaling relationships, but some general patterns across landscapes are identifiable. In contrast with Type I metrics, the values of Type II metrics at different extents can not be accurately predicted based on only a few data points.

Patch Richness	<ul style="list-style-type: none"> These metrics tend to show staircase-like responses to increasing extent, but the exact shape the response curve varies from one landscape to another.
Patch Size Standard Deviation	
Patch Size Coefficient of Variation	
Area-Weighted Mean Shape Index	<ul style="list-style-type: none"> The direction of analysis usually has pronounced effects.
Area-Weighted Mean Patch Fractal Dimension	

Type III (Extent): Metrics showing erratic responses.

- The response curves of these metrics do not show consistent patterns across different landscapes. As a result, general scaling functions seem impossible to derive. Thus, the extrapolation and interpolation of these metrics must explicitly consider the spatial structure of the landscapes.

Patch Density	
Edge Density	The response curves vary considerably among different landscapes, and even for the same landscape these metrics usually do not show simple scaling relations.
Landscape Fractal Dimension	
Mean Patch Size	
Largest Patch Index	<ul style="list-style-type: none"> MPFD and MSI are relatively insensitive to changing extent.
Contagion	
Mean Patch Shape Index	<ul style="list-style-type: none"> The direction of analysis usually has pronounced effects.
Mean Patch Fractal Dimension	

patch types in combination with the geometric increase in landscape area as extent became larger. While the general shape of the SHDI response curve seemed to fit a logarithmic function, it also exhibited staircase-like features due to the effect of PR (Figure 5).

Type II metrics in relation to changing extent included PR, PSSD, PSCV, AWMSI, and AWMFD. Note that SHDI could also be put into this category, but was classified as Type I because a simple scaling relation with a relatively high degree of consistency and accuracy could be derived. A salient characteristic of the Type II metrics was their tendency to exhibit a staircase-like pattern. The steps in each of these curves seem to corresponded to the same or similar values of extent for the same landscape. An exception was with the fine-grained, natural landscape (Boreal), in which even the smallest extent included all the vegetation types in the landscape, resulting in a constant PR value for all extents examined (Figure 5).

Type III metrics for changing extent included PD, ED, DLFD, MPS, LPI, CONT, MSI, and MPFD. These metrics did not show consistent patterns across different landscapes. As a result, deriving explicit scaling functions was not possible. For example, although NP and TE scaled up nicely following a simple power function, PD and ED did not. These two metrics behaved similarly across landscapes, but the shape of their response curves varied considerably. As in the case of changing grain size, MPFD and MSI responded to changing extent rather similarly (which was visually evident when both curves were enlarged or rescaled). They showed varying response patterns among different landscapes, but eventually stabilized as extent further increased. In general, CONT could decrease or increase with expanding extent, depending on the specifics of the landscape (Figure 5). In a similarly unpredictable way, DLFD exhibited various patterns: relatively constant over a wide range of extent, initial increase or decrease followed by relatively small changes, or considerable changes with increasing extent (Figure 5).

The effects of changing the direction of analysis (or starting position) on pattern analysis have long been recognized, particularly, in vegetation analysis using blocked quadrat variance methods (e.g., Greig-Smith (1983) and Dale (1983)) and geostatistical analysis (the problem of anisotropy; e.g., Atkinson (1993) and Leduc et al. (1994), Dale (1983)). However, we are not aware of any study that has directly

and systematically addressed the question of how changing directions of analysis or sampling affect scale-landscape metric relations when extent is varied. Our results showed that not only did changing extent, but also the direction of analysis, significantly affect the values of landscapes metrics. In general, most landscape metrics showed large differences at smaller extents among the four directions, and the differences became smaller and eventually disappeared as the overlapped area continued to increase (Figure 6). In the case of the Minden and Washoe landscapes for which the largest extent was square-shaped, a complete convergence occurred, as expected, when the overlapped area along the four directions approached 100%. Only a partial convergence was achieved for the Phx_1 landscape because a rectangular area (1500 by 2447 pixels; see Figure 1D) was used. Type I metrics were most robust in that their scaling relationships remained largely valid although the parameter values in the scaling equations among the four directions did vary considerably. Landscape metrics of Type II and Type III showed the most pronounced directionality. It was interesting to notice that four response curves for the Minden landscape formed two groups: NW-> SE and SW-> NE as one group and SE-> NW and NE-> SW as the other (Figure 6). The two curves in each group resembled each other rather closely. This apparently was indicative of the relatively symmetric landscape pattern: two similar east-west gradients converged at the center of the landscape. Such grouping did not occur for Washoe and Phx_1, implying a higher degree of structural anisotropy in these landscapes.

The divergence of the response curves along different directions was a result of the anisotropy of landscape patterns. The characteristics of the curves and their relationships together carry useful information on landscape structure. For example, suppose that landscape pattern is completely isotropic, then the response curves of all metrics should be identical. However, isotropy in all directions is at best an idealized situation for real landscapes. On the other hand, if a landscape has a relatively symmetric pattern along a direction (e.g., two gradients converge at the center of a landscape), then the four response curves along diagonal directions should be of two forms, each of which contains two similar curves (e.g., Figure 6). If a landscape has a dominant gradient, the two opposite directions along the gradient should exhibit greatest differences in landscape metrics. However, most real landscapes have complex

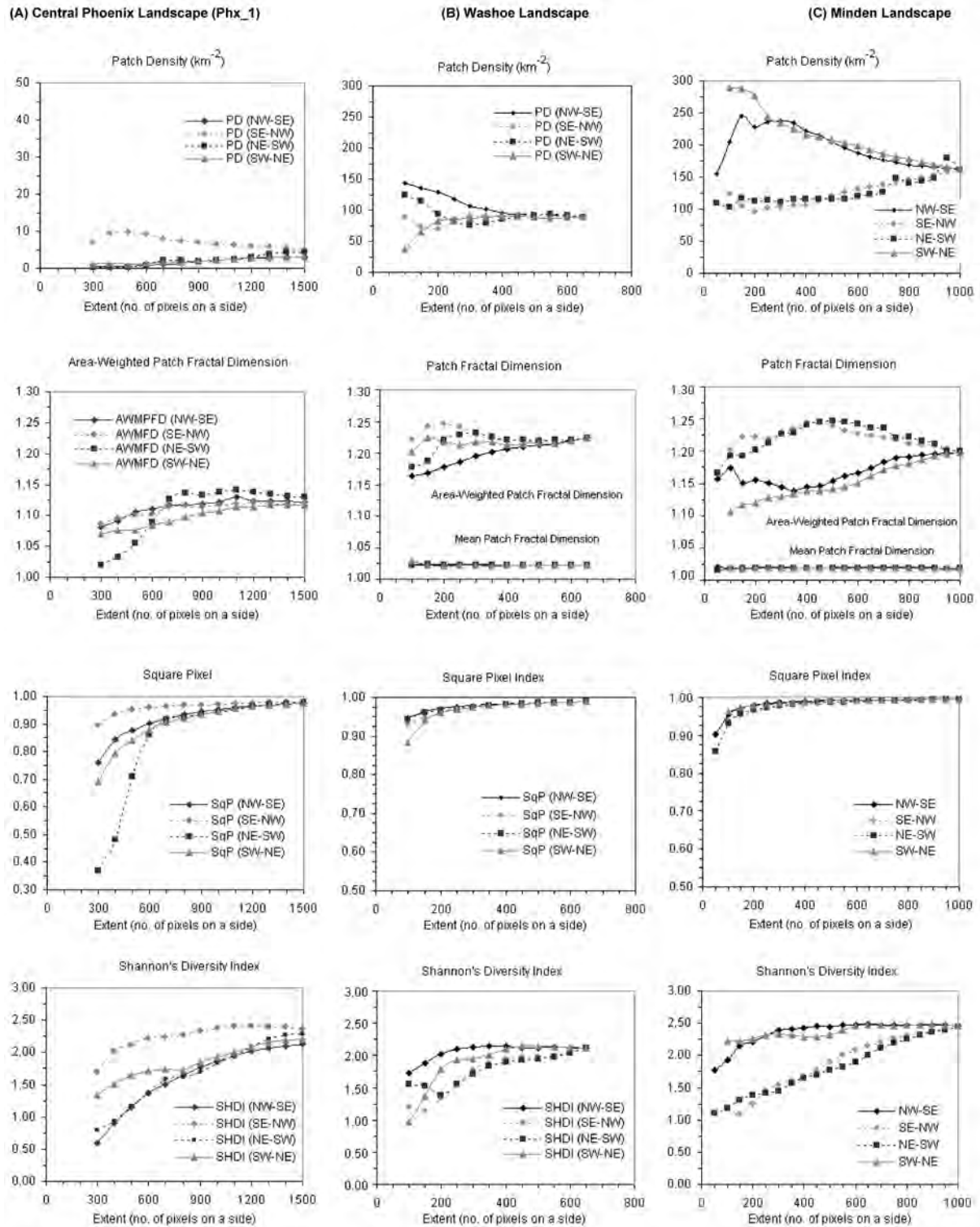


Figure 6. Effects of changing the direction of analysis or sampling on landscape indices and their scalograms: (A) the central Phoenix urban landscape, (B) the Washoe landscape in the Great Basin, and (C) the Minden landscape in the Great Basin.

patterns that do not neatly follow into these categories. In general, the differences among response curves in different directions ought to increase with decreasing spatial symmetry or increasing anisotropy. As a consequence, the exact characteristics of the response curves in different directions may vary unpredictably. Nevertheless, the discrepancies themselves may be of interest to landscape ecologists who want to understand the directionality or orientation of the multi-scale patterns of landscapes.

Discussion

Modifiable areal unit problem (MAUP)

The problems of scale effects and spatial aggregation had long been studied even before landscape ecology achieved its prominent status in the 1980s. Much of the research relevant to scale effects was carried out under the umbrella term, the modifiable areal unit problem (MAUP), in geography and social sciences (see Openshaw (1984) and Jelinski and Wu (1996), Marceau (1999) for reviews). MAUP includes two separate, but interrelated problems with spatial analysis of area-based data: the scale problem and zoning problem. The scale problem occurs when the same set of areal data is aggregated into a smaller numbers of larger areal units (i.e., changing grain size), whereas the zoning problem is encountered when areal units at a given scale are combined into different zones in different ways without changing the grain or extent. In this study, we only dealt with the scale problem in terms of both grain size and extent, but not the zoning problem.

Numerical relationships among certain landscape metrics

Some of the landscape metrics are numerically related or statistically correlated, and these relationships should be reflected in the response curves of these landscape metrics. For example, because $LSI = 0.25 TE/\sqrt{TA}$ (where TA is the total area of the landscape), LSI and TE must have the same type of response curves for changing grain size (TA remains constant for the analysis of changing grain size). In the case of changing extent, if TE increases as a power function ($y = \alpha x^\beta$) with extent (in the number of pixels on a side), LSI should follow a scaling function of the form, $y \propto x^{\beta-1}$. Then, if β is close to 2, then LSI

should behave linearly. Similarly, for $PD = NP/TA$ and $ED = TE/TA$, NP and PD , and TE and ED should have the same type of response curves to changing grain size (a monotonically decreasing power function). Yet, in the case of changing extent, the behavioral pattern of NP and TE diverges from that of PD and ED . The former is an increasing power function, but the latter takes the form of $y \propto x^{\beta-2}$. Due to the variations in β among different landscapes and changes in patch size, shape and distribution within the same landscape as extent is altered, the changes in PD and ED no longer follow any simple scaling relations. In addition, because PR and PRD are directly related as $PRD = PR/TA$, in the case of changing grain size, PRD should mimic PR 's pattern, although the sharp changes in PR become smoother in PRD . However, in the case of changing extent, TA increases exponentially, PR increases only arithmetically, and thus PRD , in general, obeys a decreasing power function (but significant deviations were found with the two Phoenix landscapes along certain directions of analysis). Because $PSCV = (PSSD/MPS)100$, any two of the three response curves will determine the third one. Finally, LSI and SqP can be numerically related to each other as $LSI = (1 - SqP)^{-1}$. Thus, the response curves of LSI and SqP should reflect this relationship.

On diversity, contagion, and fractal dimension indices

In one of the earliest and most widely cited studies of scale effects in landscape ecology, Turner et al. (1989) investigated the effects of changing grain size and extent on dominance and contagion indices. They found that, in general, both indices decreased with increasing grain size and increased with increasing extent. Our results showed that Shannon's diversity ($SHDI$), a related index to dominance ($D = H_{max} - SHDI$), decreased with increasing grain size, but increased with expanding extent. These results were not necessarily at odds because, as Turner et al. (1989) noted, dominance was more variable than diversity in response to changing grain size. We found that contagion decreased with both increasing grain size and extent although increases over certain short ranges of scale were observed. One exception was that contagion actually increased monotonically with increasing grain size (Figure 4). The discrepancy between Turner et al.'s and our results on contagion might be due partly to the different formulas of the metric used in

these studies. Turner et al. (1989) used the formula of contagion originally proposed by O'Neill et al. (1988), whereas FRAGSTATS uses the 'relative contagion' by Li and Reynolds (1993). The discrepancy might also be attributable to the different aggregation methods (iterative aggregation in the former and independent aggregation in the latter; R. H. Gardner, pers. comm.). At any rate, because the value of contagion is affected by the number and evenness of patch types, spatial arrangement of patches, and grain size (Li and Reynolds 1993; Riitters et al. 1996; Frohn 1998), a general scaling relationship does not seem to exist across different landscapes.

Riitters et al. (1995, 1996) reported that the contagion index was highly correlated with diversity indices. Our results showed that the response curves of diversity and contagion to changing grain size and extent also seemed correlated, but exceptions did occur (see Figure 4). Wickham and Riitters (1995) investigated the effects of changing pixel sizes on several indices of diversity and evenness, and found that all of them were insensitive to changing grain size. The insensitivity, as they suggested, might be due to the fact that only a narrow range of grain sizes was considered (4 pixel sizes: $4 \times 4 \text{ m}^2$, $12 \times 12 \text{ m}^2$, $28 \times 28 \text{ m}^2$, and $80 \times 80 \text{ m}^2$). In contrast, the total number of grain sizes in this study was 24, ranging from $30 \times 30 \text{ m}^2$ to $3000 \times 3000 \text{ m}^2$). By visually examining the beginning part of each curve in Figure 4, it seems that changing grain size even over a short range with relatively fine-resolution data sets may still result in pronounced effects on some landscape metrics. This is especially true for those metrics that follow a decreasing power-law function.

Based on remote sensing data of the northern Wisconsin lake district at different spatial resolutions (20 m for SPOT, 30 m for Landsat TM, and 1100 m for AVHRR), Benson and Mackenzie (1995) found that, with decreasing spatial resolution the number of lakes and their percent coverage decreased, but the average area and perimeter of lakes and landscape fractal dimension increased. Also, after systematically aggregating the fine resolution data from 20 m to 1100 m following the majority rule they found that the values of the landscape metrics from the simulated data closely matched those from the three original remote sensing data sets. In contrast, we found that the behavior of landscape fractal dimension in response to changing grain size was rather inconsistent (Figures 3 and 4); (Tables 4 and 5).

Frohn (1998) compared contagion and fractal dimension (DLFD) with two so-called 'new' landscape metrics, patch-per-unit area (PPU) and square pixel (SqP), in terms of their responses to changing grain size or spatial resolution of remote sensing data. PPU is simply the number of patches per square kilometer, which is identical to the formula of patch density in FRAGSTATS, expressed as the number of patches per 100 ha ($1 \text{ km}^2 = 100 \text{ ha}$). SqP is just another form of perimeter-area ratio, and is mathematically related to landscape shape index (LSI) as discussed above. Our study seems to suggest that both indices showed limitations as a measure of the shape complexity of a landscape. While the shape complexity of a landscape should continue to decrease with increasing grain size, LSI seemed to exhibit an asymptotic behavior as grain size became relatively large. Similarly, with increasing extent, SqP quickly approached the maximum value of 1 although landscape heterogeneity continued to increase (Figure 5). In addition, Frohn (1998) suggested to replace contagion and fractal dimension with PPU and SqP. While the range of grain sizes he used was narrower (from $30 \times 30 \text{ m}$ to $1000 \times 1000 \text{ m}$), the erratic and generally unpredictable behavior of contagion and fractal dimension among different landscapes reported by Frohn (1998) was confirmed by our results. But, it needs to be pointed out that neither PPU nor SqP is a spatially explicit index. Although one needs to be cautious about the use and interpretation of contagion (Riitters et al. 1996), it incorporates both compositional and configurational attributes of landscapes in its formulation, and thus provides extra information that PPU (patch density) does not.

Future research directions

Since the study landscapes (from natural to highly urbanized) represent a wide range of spatial patterns in terms of the relative abundance and spatial distribution of patch types, the three general response patterns seem robust. However, these results need to be further verified by additional studies with both real and artificial landscapes. In particular, detailed analyses with simulated landscapes with known and systematically varying properties (e.g., Gardner et al. (1987) and Lavorel et al. (1993), Li and Reynolds (1994)) would be particularly useful to elucidate how landscape metrics respond to scale changes along with other landscape pattern variables (which is part of our on-going research). For example, increasing

extent usually is accompanied by an increasing number of patch types in real landscapes, but one can control patch richness in simulated landscapes. In this study, the patch richness of the boreal forest landscape remained constant over the entire range of varied extents, yet most landscape metrics showed similar response patterns as compared to the other landscapes (Figure 5). Nevertheless, future research is needed to tease out the 'pure' effects of changing extent and grain size, which requires rigorous experimental designs with artificial data sets. Saura and Martinez-Millan (2001) have recently provided such an example with changing extent for binary landscapes.

This paper covers only landscape-level metrics, which are computed for the entire landscape as a whole and thus measures of the landscape pattern rendered by all patch types (or classes). In contrast, class-level metrics are 'patch type-specific landscape metrics', which are computed for each patch type individually over the landscape (McGarigal and Marks 1995). Many ecological applications require information on the abundance and configuration of different habitat or cover types that is provided by class-level metrics. Do class-level metrics show similar patterns to those found for landscape-level metrics in terms of their responses to changing grain size and extent? We are currently carrying out this analysis for the same landscapes used in this study, and the results will be reported elsewhere. In addition, a number of studies have shown that different aggregation methods (e.g., the majority rule, random selection, regular selection) may have significant effects on land cover classification and landscape pattern (e.g., Justice et al. (1989) and Marceau et al. (1994), Bian and Butler (1999)). Each aggregation method has its pros and cons, of which an excellent discussion is provided in Turner et al. (2001). It would be interesting to investigate how these different aggregation methods (and also the iterative vs. independent aggregation schemes) affect the characteristics of landscape metric scalograms (R. H. Gardner, pers. comm.).

Conclusions

Our results demonstrated that changing grain size and extent both had significant effects on landscape met-

rics. The responses of landscape metrics to changing scale (grain size or extent) can be summarized into three general types. Type I metrics showed predictable patterns, and their scaling relations can be represented by simple equations (linear, power-law, or logarithmic functions). Type II metrics exhibited staircase-like responses with changing scale. Because the number of steps and their height in the response curves were not predictable, scaling functions were not possible to be derived. Type III metrics behaved erratically in response to changing scale, suggesting no consistent scaling relations among different landscapes. The above conclusions do not mean that all Type II and III metrics never exhibit any kind of general patterns. Indeed, some of them did show some qualitatively consistent responses, while others did not (Table 6). The direction of analysis also had significant effects on landscape pattern analysis which, in general, were not predictable *a priori*.

The results of our study suggest that the effects of changing grain size tend to be more predictable than those of changing extent. Type I metrics represent those landscape features that can be extrapolated or interpolated across spatial scales relatively readily and accurately using only a few to several data points, whereas Type II and III metrics represent those of which such simple scaling relations do not exist. In this case, the explicit consideration of the specifics of landscape pattern would be necessary for scaling spatial pattern. The scale-dependence of landscape metrics supports the claim that there is no single 'correct' or 'optimal' scale for characterizing and comparing landscape patterns (e.g., Levin (1992) and Wu and Loucks (1995)). Therefore, we suggest that landscape metric scalograms (the response curves of landscape metrics to changing grain size or extent), instead of the single values of the metrics, should be used for characterizing, comparing, and monitoring landscape patterns. It seems that landscape metric scalograms are more likely to be successful for linking landscape pattern to ecological processes because both pattern and process in ecological systems often operate on multiple scales.

Table 6. Comparison of Type II and III metrics and their behavioral characteristics in both cases of changing grain size and extent.

Type II metrics	Metric	General Pattern
Changing grain size	PR	<ul style="list-style-type: none"> ● A stepping-down staircase curve ● Details of the curve vary among different landscapes
	PRD	
	SHDI	
Changing extent	PR	<ul style="list-style-type: none"> ● A stepping-up staircase curve ● Details of the curve vary among landscapes, and are sensitive to the direction of analysis ● Mostly, a stepping-up staircase curve, but changing the direction of analysis may alter the general pattern ● Details of the curve may vary over different ranges of scale for the same landscape and among different landscapes
	PSSD	
	PSCV	
	AWMSI	
	AWMFD	
Type III metrics		
Changing grain size	CONT	<ul style="list-style-type: none"> ● No general pattern ● Generally decreasing or insensitive to changing scale ● Generally decreasing with variations over certain ranges of grain size (usually when grain size is small)
	MPFD	
	DLFD	
Changing extent	MSI	<ul style="list-style-type: none"> ● No general pattern among different landscapes Sensitive to the direction of analysis ● No general pattern Relatively insensitive to the direction of analysis ● Generally decreasing with local variations over certain ranges of scale Sensitive to the direction of analysis
	DLFD	
	MSI	
	PD	
	ED	
	MPS	
	MPFD	
	CONT	
LPI		

Acknowledgements

We would like to thank Ellen Ellis, Michael Limb, Yuanbo Liu, and Matt Luck for their assistance with the preparation of the data sets used in this study. We are also grateful to Fangliang He, Darrel Jenerette, Habin Li, and Matt Luck for their comments on an earlier draft of the paper. We especially appreciate the comments and suggestions by R. H. Gardner and two anonymous reviewers which led to substantial im-

provements of the manuscript. This research was supported in part by grants from US-EPA (R827676-01-0), USDA (NRICGP 95-37101-2028) and US-NSF (DEB 97-14833, CAP-LTER).

References

- Atkinson P.M. 1993. The effect of spatial resolution on the experimental variogram of airborne MSS imagery. *International Journal of Remote Sensing* 14: 1005–1011.
- Benson B.J. and Mackenzie M.D. 1995. Effects of sensor spatial resolution on landscape structure parameters. *Landscape Ecology* 10: 113–120.
- Bian L. and Butler R. 1999. Comparing effects of aggregation methods on statistical and spatial properties of simulated spatial data. *Photogrammetric Engineering & Remote Sensing* 65: 73–84.
- Buckley R.C. 1985. Distinguishing the effects of area and habitat type on island plant species richness by separating floristic elements and substrate types. *Journal of Biogeography* 12: 527–535.
- Dale M.R.T. 1983. *Spatial Pattern Analysis in Plant Ecology*. Cambridge University Press, Cambridge, UK.
- Frohn R.C. 1998. *Remote Sensing for Landscape Ecology: New Metric Indicators for Monitoring, Modeling, and Assessment of Ecosystems*. Lewis Publishers, Boca Raton, Florida, USA.
- Gardner R.H. 1998. Pattern, process, and the analysis of spatial scales. In: Peterson D.L. and Parker V.T. (eds), *Ecological Scale*. Columbia Univ. Press, New York, New York, USA, pp. 17–34.
- Gardner R.H., Milne B.T., Turner M.G. and O'Neill R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. *Landscape Ecology* 1: 19–28.
- Greig-Smith P. 1983. *Quantitative Plant Ecology*. University of California Press, Berkeley, California, USA.
- He F. and Legendre P. 1994. Diversity pattern and spatial scale: A study of a tropical rain forest of Malaysia. *Environmental & Ecological Statistics* 1: 265–286.
- Jelinski D.E. and Wu J. 1996. The modifiable areal unit problem and implications for landscape ecology. *Landscape Ecology* 11: 129–140.
- Jenerette G.D. and Wu J. 2002. Analysis and simulation of land use change in the central Arizona – Phoenix region. *Landscape Ecology* 16: 611–626.
- Justice C.O., Markham B.L., Townshend J.R.G. and Kennard R.L. 1989. Spatial degradation of satellite data. *International Journal of Remote Sensing* 10: 1539–1561.
- Lavorel S., Gardner R.H. and O'Neill R.V. 1993. Analysis of pattern in hierarchically structured landscapes. *Oikos* 67: 521–528.
- Leduc A., Prairie Y.T. and Bergeron Y. 1994. Fractal dimension estimates of a fragmented landscape: Sources of variability. *Landscape Ecology* 9: 279–286.
- Levin S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943–1967.
- Li H. and Reynolds J.F. 1993. A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecology* 8: 155–162.
- Li H. and Reynolds J.F. 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75: 2446–2455.
- Luck M. and Wu J. 2002. A gradient analysis of urban landscape pattern: A case study from the Phoenix Metropolitan region of USA. *Landscape Ecology* 17: 327–329, (accepted).
- MacArthur R.H. and Wilson E.O. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press, Princeton, New Jersey, USA.
- Marceau D.J., Howarth P.J. and Gratto D.J. 1994. Remote Sensing and the measurement of geographical entities in a forested environment. 1. The scale and spatial aggregation problem. *Remote Sensing of Environment* 49: 93–104.
- Marceau D.J. 1999. The scale issue in social and natural sciences. *Canadian Journal of Remote Sensing* 25: 347–356.
- McGarigal K. and Marks B.J. 1995. FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. Gen. Tech. Rep. PNW-GTR-351. USDA-Forest Service, Portland, Oregon, USA.
- Meentemeyer V. and Box E.O. 1987. Scale effects in landscape studies. In: Turner M.G. (ed.), *Landscape Heterogeneity and Disturbance*. Springer-Verlag, New York, New York, USA, pp. 15–34.
- Moody A. and Woodcock C.E. 1995. The influence of scale and the spatial characteristics of landscapes on land-cover mapping using remote sensing. *Landscape Ecology* 10: 363–379.
- O'Neill R.V., Gardner R.H., Milne B.T., Turner M.G. and Jackson B. 1991. Heterogeneity and Spatial Hierarchies. In: Kolasa J. and Pickett S.T.A. (eds), *Ecological Heterogeneity*. Springer-Verlag, New York, New York, USA, pp. 85–96.
- O'Neill R.V., Hunsaker C.T., Timmins S.P., Timmins B.L., Jackson K.B., Jones K.B. et al. 1996. Scale problems in reporting landscape pattern at the regional scale. *Landscape Ecology* 11: 169–180.
- O'Neill R.V., Krummel J.R., Gardner R.H., Sugihara G., Jackson B., DeAngelis D.L. et al. 1988. Indices of landscape pattern. *Landscape Ecology* 1: 153–162.
- Openshaw S. 1984. *The Modifiable Areal Unit Problem*. Geo Books, Norwich, UK.
- Qi Y. and Wu J. 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landscape Ecology* 11: 39–49.
- Riitters K.H., O'Neill R.V., Hunsaker C.T., Wickham J.D., Yankee D.H., Timmins K.B.J. et al. 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecology* 10: 23–39.
- Riitters K.H., O'Neill R.V., Wickham J.D. and Jones K.B. 1996. A note on contagion indices for landscape analysis. *Landscape Ecology* 11: 197–202.
- Saura S. and Martinez-Millan J. 2001. Sensitivity of landscape pattern metrics to map spatial extent. *Photogrammetric Engineering & Remote Sensing* 67: 1027–1036.
- Turner M.G. 1989. Landscape ecology: The Effect of pattern on process. *Annual Review of Ecology and Systematics* 20: 171–197.
- Turner M.G., Gardner R.H. and O'Neill R.V. 2001. *Landscape Ecology in Theory and Practice: Pattern and Process*. Springer-Verlag, New York, New York, USA.
- Turner M.G., O'Neill R.V., Gardner R.H. and Milne B.T. 1989. Effects of changing spatial scale on the analysis of landscape pattern. *Landscape Ecology* 3: 153–162.
- Wickham J.D. and Riitters K.H. 1995. Sensitivity of landscape metrics to pixel size. *Int. J. Rem. Sens.* 16: 3585–3595.
- Wiens J.A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.
- Williamson M. 1988. Relationship of species number to area, distance and other variables. In: Myers A.A. and Giller P.S. (eds), *Analytical Biogeography*. Chapman and Hall, London, UK, pp. 91–115.
- Woodcock C.E. and Strahler A.H. 1987. The factor of scale in remote sensing. *Remote Sensing of Environment* 21: 311–332.

- Wu J. 1999. Hierarchy and scaling: Extrapolating information along a scaling ladder. *Canadian Journal of Remote Sensing* 25: 367–380.
- Wu J., Jelinski D.E., Luck M. and Tueller P.T. 2000. Multiscale analysis of landscape heterogeneity: Scale variance and pattern metrics. *Geographical Information Systems* 6: 6–19.
- Wu J. and Levin S.A. 1994. A spatial patch dynamic modeling approach to pattern and process in an annual grassland. *Ecological Monographs* 64: 447–464.
- Wu J. and Loucks O.L. 1995. From balance-of-nature to hierarchical patch dynamics: A paradigm shift in ecology. *Quarterly Review of Biology* 70: 439–466.
- Wu J. and Vankat J.L. 1991. A System Dynamics model of island biogeography. *Bulletin of Mathematical Biology* 53: 911–940.
- Wu J. and Vankat J.L. 1995. Island biogeography: Theory and applications. In: Nierenberg W.A. (ed.), *Encyclopedia of Environmental Biology*. Academic Press, San Diego, California, USA, pp. 371–379.