available at www.sciencedirect.com

ScienceDirect

journal homepage: www.elsevier.com/locate/ecolind

ELSEVIER

Parsimony in landscape metrics: Strength, universality, and consistency

Samuel A. Cushman *, Kevin McGarigal, Maile C. Neel*

USDA Forest Service, Rocky Mountain Research Station, 800 E Beckwith, MIssoula, MA 59801, United States

ARTICLE INFO

Article history:
Received 11 September 2007
Received in revised form
30 November 2007
Accepted 3 December 2007

Keywords:
Landscape structure
Landscape pattern
Landscape monitoring
Ecological indicators
FRAGSTATS
Landscape metrics

ABSTRACT

Ecologists can be overwhelmed by the number of metrics available to quantify landscape structure. Clarification of interrelationships and redundancy is needed to guide metric selection and interpretation for the purpose of landscape monitoring. In this study we identified independent components of class- and landscape-level structure in multiple landscapes in each of three large and geographically disjunct study areas. We used FRAGSTATS and principal components analysis (PCA) to identify independent components of landscape structure, and cluster analysis to group the components. We then calculated the universality, strength, and consistency of the identified landscape structure components. At the class-level we identified 24 independent configuration components. Seven of these components were nearly universal and consistent in interpreted meaning. At the landscape-level there were 17 independent structure components. Eight of these components were universal and consistent. These results indicate that there are consistent combinations of metrics that universally describe the major attributes of landscape structure at the class- and landscape-levels.

Published by Elsevier Ltd.

1. Introduction

Over the past two decades there has been a proliferation of statistical measures of landscape structure (O'Neill et al., 1988; Turner, 1990; Turner and Gardner, 1991; Baker and Cai, 1992; Li and Reynolds, 1995; McGarigal and Marks, 1995; Gustafson, 1998; He et al., 2000; Jaeger, 2000; McGarigal et al., 2002). While this effort has provided scientists with a wealth of information about landscape structure, it has also created a potentially large source of confusion. The proliferation of metrics poses a serious challenge for the investigator to determine how many components of landscape structure are relevant and which metrics should be used to represent those components. It is desirable to use the smallest number of independent metrics which sufficiently quantify landscape structure. However, it is difficult to know a priori what this set of metrics will be for any landscape.

Metric selection is also hampered by several characteristics of the metrics themselves. First, there is seldom a one-to-one (i.e., linear) relationship between metric values and landscape structure (Gustafson and Parker, 1992; Hargis et al., 1998; Baldwin et al., 2001; McGarigal, 2002; Neel et al., 2004). Further, many metrics simultaneously measure multiple aspects of structure, confounding landscape composition (i.e., the variety and abundance of patch types within the landscape) and configuration (i.e., the spatial character and arrangement, position, or orientation of patches within the class or landscape) (McGarigal and Marks, 1995; Gustafson, 1998). In addition, some metrics are inherently redundant because they are alternate ways of representing the same basic

* *Corresponding author*. Present address: USDA Forest Service, Rocky Mountain Research Station, 800 East Beckwith, PO Box 8089, Missoula, MT 59807, United States. Tel.: +1 406 546 6379.

E-mail address: scushman@fs.fed.us (S.A. Cushman).

1470-160X/$ – see front matter. Published by Elsevier Ltd.
doi:10.1016/j.ecolind.2007.12.002

information (e.g., mean patch size and patch density). In other cases, metrics may be empirically redundant, not because they fundamentally measure the same aspect of structure, but because for the landscapes under investigation, different aspects of landscape structure are correlated.

Previous studies have attempted to determine if the major components of landscape structure can be represented by a parsimonious suite of independent metrics (e.g., McGarigal and McComb, 1995; Riitters et al., 1995; Cain et al., 1997; Scanes and Bunce, 1997; Tinker et al., 1998; Griffith et al., 2000; Lausch and Herzog, 2002; Cifaldi et al., 2004; Linke and Franklin, 2006; Schindler et al., 2008). Each of these studies suggested that patterns can be characterized by relatively few components; however, the identified components differed among the studies. This lack of concordance in important landscape structure components raises the possibility that there are no fundamentally important aspects of landscape structure and instead that structure patterns are peculiar to specific landscapes. The apparent lack of fundamental components is, however, more likely a consequence of the fact that the different studies did not use the same pool of metrics and used different methods to identify components. McGarigal and McComb (1995), for example, identified a set of components based on a small number of class-level metrics in 30 landscapes within a single geographical area. Prior to factor analysis, the percent of landscape in the focal class was partialled out to remove effects of class area on landscape configuration. In contrast, Riitters et al. (1995) quantified redundancy of landscape-level metrics from 85 landscapes sampled across a vast geographical space. However, their analysis did not explicitly assess consistency of component meaning or universality of component presence among regions, nor did it separate effects of area and configuration.

The overall goal of this study was to identify independent components of landscape structure in three geographically isolated regions and to determine whether the identified components were idiosyncratic or whether components were common across class types and regions. Structural components analyzed in this study are principal components (i.e., composite variables). They are the major independent dimensions of landscape structure that exist among the measured landscapes. We evaluated the importance of each component using three measures: universality, strength, and consistency. Universality is the percentage of classes or regions in which a component is found. Strength is assessed as the average variance explained by a structure component across classes and regions. Consistency measures the stability of component interpretation among classes and regions.

We combine the strengths of the previous studies by sampling a large number of landscapes from a variety of physiographic provinces (e.g., Riitters et al., 1995; Cain et al., 1997) and by separating effects of landscape composition from configuration at the class-level (McGarigal and McComb, 1995). We improve on those studies by including a larger number of metrics, by examining landscape- and class-level metrics separately, and by evaluating the importance of landscape structure gradients across classes and regions. Our analysis did not focus on functional metrics that are explicitly related to ecological processes. By definition, functional metrics change in definition and interpretation with changes in the goals and methods of study. We focused on 'objective' structure metrics because they are constant among studies. Analyses similar to this, but using functional metrics, would be useful within the context of particular ecological analyses.

2. Methods

2.1. Study areas

The study was conducted using landscape maps from three large, disjunct geographical regions in the United States. The first region included an approximately 15,000 km^2 portion of western Massachusetts that is dominated by mixed deciduous–coniferous forests and characterized by rolling hills, agricultural valleys and scattered urban and residential development. It includes the Berkshire Hills, Connecticut River Valley, and Worcester Plateau regions of Massachusetts. The landcover map used in this analysis was created from 1999 aerial photography with a minimum mapping unit of 0.1 acre. We converted the original vector coverage into a grid with a 30 m cell size and reclassified it into seven cover classes to ensure adequate distribution of classes across sub-landscapes (see below). The seven classes included forest, water, grassland, cropland, urban, high-density residential, and low-density residential.

The second region was the 8480 km^2 San Juan National Forest in southwestern Colorado. This mountainous landscape has rugged topography and extreme elevational relief. Landcover is zonal, with Ponderosa pine (*Pinus ponderosa*) forest in the lower elevations, mixed-coniferous and aspen (*Populus tremuloides*) forest in the middle elevations, and spruce-fir forest (primarily *Picea engelmannii* and *Abies lasiocarpa*) and treeless alpine communities at the highest elevations. The landcover map used in this analysis was derived from the USDA Forest Service Integrated Resources Inventory (IRI) and Resources Information System (RIS) database. The coverage was a grid with a 25 m cell size. We maintained the original resolution to avoid errors related to resampling and reclassified it into four cover classes to ensure adequate distribution of all classes across sub-landscapes. The four cover classes included forest, water, riparian, and non-forested.

The third region was an approximately 20,000 km^2 area of central Idaho. This region is also mountainous with zonal landcover. The landcover map was developed by the Idaho Gap Analysis project with 30-m pixels. We reclassified the map into five cover classes, including forest, rock, riparian, grass, and shrub with the same goal of ensuring adequate distribution of all classes across sub-landscapes.

We superimposed a square grid with 256 cells per side and clipped each of the three regional landcover maps into non-overlapping sub-landscapes of these dimensions. This process resulted in 155 sample landscapes for western Massachusetts, 152 sample landscapes for the San Juan National Forest, and 221 for central Idaho. We chose this sub-landscape size to ensure adequate representation of all classes in most sampled landscapes, while yielding a sufficient number of landscapes to provide an approximately three-to-one sample to variable ratio for principal components analysis (PCA).

Table 1 – List of the 49 class-level (C) and 54 landscape-level (L) landscape structure metrics calculated for the analysis (see McGarigal et al., 2002 for a complete description of each metric)

Metric number	Level	Acronym	Name
0	C, L	PLAND	Proportion of landscape
1	C, L	PD	Patch density
2	C, L	LPI	Largest patch index
3	C, L	ED	Edge density
4	C, L	LSI	Landscape shape index
5	C, L	AREA_MN	Mean patch size
6	C, L	AREA_AM	Area–weighted mean patch size
7	C, L	AREA_CV	Patch size coefficient of variation
8	C, L	GYRATE_MN	Mean radius of gyration
9	C, L	GYRATE_AM	Correlation length
10	C, L	GYRATE_CV	Radius of gyration coefficient of variation
11	C, L	SHAPE_MN	Mean shape index
12	C, L	SHAPE_AM	Area–weighted mean shape index
13	C, L	SHAPE_CV	Shape index coefficient of variation
14	C, L	FRAC_MN	Mean fractal dimension
15	C, L	FRAC_AM	Area–weighted mean fractal dimension
16	C, L	FRAC_CV	Fractal dimension coefficient of variation
17	C, L	PARA_MN	Mean perimeter–area ratio
18	C, L	PARA_AM	Area–weighted mean perimeter–area ratio
19	C, L	PARA_CV	Perimeter–area ratio coefficient of variation
20	C, L	DCAD	Disjunct core area density
21	C, L	CORE_MN	Mean core area
22	C, L	CORE_AM	Area–weighted mean core area
23	C, L	CORE_CV	Core area coefficient of variation
24	C, L	DCORE_MN	Mean disjunct core area
25	C, L	DCORE_AM	Area–weighted mean disjunct core area
26	C, L	DCORE_CV	Disjunct core area coefficient of variation
27	C, L	CAI_MN	Mean core area index
28	C, L	CAI_AM	Area–weighted mean core area index
29	C, L	CAI_CV	Core area coefficient of variation
30	C, L	PROX_MN	Mean proximity index
31	C, L	PROX_AM	Area–weighted mean proximity index
32	C, L	PROX_CV	Proximity index coefficient of variation
33	C, L	SIMI_MN	Mean similarity index
34	C, L	SIMI_AM	Area–weighted mean similarity index
35	C, L	SIMI_CV	Similarity coefficient of variation
36	C, L	ENN_MN	Mean nearest neighbor distance
37	C, L	ENN_AM	Area–weighted mean nearest neighbor distance
38	C, L	ENN_CV	Nearest neighbor distance coefficient of variation
39	C, L	CWED	Contrast weighted edge density
40	C, L	TECI	Total edge contrast index
41	C, L	ECON_MN	Mean edge contrast
42	C, L	ECON_AM	Area–weighted mean edge contrast
43	C, L	ECON_CV	Edge contrast coefficient of variation
44	C, L	CLUMPY	Clumpiness index
45	C, L	PLADJ	Proportion of like adjacencies
46	C, L	IJI	Interspersion/juxtaposition index
47	C, L	COHESION	Patch cohesion
48	C, L	SPLIT	Splitting index
49	C, L	AI	Aggregation index
50	L	MESH	Mesh size
51	L	DIVISION	Division index
52	L	PRD	Patch richness density
53	L	SIDI	Simpson's patch diversity
54	L	SIEI	Simpson's patch evenness

PLAND is the covariable in the partial principal components analyses at the class-level.

2.2. *Principal component analyses*

For each cover class in each sample landscape we calculated 49 class-level landscape structure metrics using the computer program FRAGSTATS version 3.2 (McGarigal et al., 2002; Table 1). We included the full range of class-level metrics available for quantifying landscape structure at the time of our analysis, after eliminating those that are computationally redundant. We conducted a partial PCA (pPCA) analysis on the correlation matrix using PROC FACTOR in SAS (SAS, 2002) for each cover class in each of the three regions. We used varimax rotation to maximize component interpretability. For each cover class, the variable PLAND (percent of the cover class in the landscape) was partialed out. The partial analysis extracts the major components in the class-level metrics that are linearly independent of the amount of that cover class present. In effect, the partial PCA removes the effect of landscape composition, and the resulting components are the major independent dimensions of landscape configuration at the class-level. We retained all components that were significant based on the latent root criterion (McGarigal et al., 2000). Due to early concerns that removing the linear relationship between PLAND and landscape structure components would obscure any known and unknown underlying nonlinear relationships, during exploratory analyses we also used nonlinear regression techniques to partial out nonlinear relationships between PLAND and each metric separately prior to PCA. The results were similar to pPCA, suggesting that within the range of real landscape patterns sampled, these nonlinearities were subordinate to the predominantly linear relationships.

We calculated 54 landscape-level metrics for each sub-landscape in each of the three regions (Table 1). As with the class-level metrics, we included the full range of available landscape-level metrics after eliminating those that were inherently redundant (McGarigal et al., 2002). We conducted a PCA separately for each of the three regions. Because there is no landscape-level measure equivalent to PLAND we did not use partial PCA. As a result, the landscape-level components confound composition and configuration.

2.3. *Polythetic agglomerative hierarchical clustering*

We used polythetic agglomerative hierarchical clustering with average linkage (SAS, 2002) to combine the individual landscape structure components extracted by PCA into groups based on factor pattern similarity. The factor pattern for a component is the list of the Pearson's correlation coefficients between each contributing metric and that component. The degree of similarity in factor patterns between two components indicates the degree of similarity of the components in terms of the landscape structure gradient they represent. To derive the distance matrices for the cluster analyses we first computed the Pearson correlation matrix between the factor patterns of each principal component to be clustered. We then subtracted each $|r|$ value in the correlation matrix from 1 so that distance values ranged from 0 for perfect correlation of factor patterns between two components, to 1 for no factor pattern correlation. We clustered all PCA components, for all cover classes, in all regions simultaneously ($N = 211$) to identify the sets of class-level structure components that were similar across cover classes and across regions. We based the final cluster membership on the inflection point of the scree-plot of fusion distances (McGarigal et al., 2000). For all subsequent class-level analyses, we used this same distance (0.59) as the cutoff for cluster membership, to ensure consistency in cluster definition rules. At the landscape-level, we conducted a single cluster analysis of all landscape-level structure components from all three study regions ($N = 35$) to group similar landscape-level structure components across all regions. As in the class-level analysis, we based the final cluster membership on the inflection point of the scree-plot of fusion distances, which in the landscape-level clustering was 0.43.

2.4. *Discriminant analysis and partial discriminant analysis*

We used weighted averaging discriminant analysis (DA) as implemented in CANOCO 4 (ter Braak and Šmilauer, 1998) to quantify the statistical significance of the identified clusters across the three regions at both the class- and landscape-levels and partial DA to quantify the influences of differences among geographical regions on the stability of the extracted landscape pattern components. At the class-level there were a sufficient number of components (samples) to use all the metrics in the DAs. At landscape-level we had more variables than samples, invalidating analysis using the full data set. To improve the sample to variable ratio for the landscape-level analysis we used forward selection in CANOCO to select the 13 most significant landscape-level metrics for inclusion in the discriminant models.

We assessed the significance of discrimination among identified clusters using Monte Carlo permutation testing with 199 permutations (ter Braak and Šmilauer, 1998). In the partial DA we included region as a set of dummy covariables to account for differences that may exist in the structure components between different regions (ter Braak and Šmilauer, 1998). The change in the variance explained and classification accuracy between the full and partial DA provide a measure of the extent of regional differences in landscape structure components.

2.5. *Universality, strength, and consistency of landscape pattern components*

We used three measures (universality, strength, and consistency) to quantify the overall importance of the landscape structure components identified with clustering and DA. *Universality* is simply the percentage of regions, for the landscape-level analysis, and region-class combinations, for the class-level analysis, in which the particular structural component was present. For example, in the class-level analysis, there are 16 possible universality scores, corresponding to the how many times the component is present among the 16 combinations of cover class and region. If a structural component exists across all the cover classes in all the regions studied, it reflects a universal dimension of landscape structure.

Strength is a measure of the average variance accounted for by a particular landscape structural component, when it is present. Thus, a component is relatively strong if it tends to explain a relatively large amount of the variance in the constituent metrics. We measured the strength of each identified structural component in two ways. First, the average eigenvalue provides a quantitative measure of the amount of variance among metrics the structural component captures on average across regions, and across all class–region combinations. Second, we computed the total variation accounted for by each structural component as a percentage

Table 2 – Summary of the class-level partial principal components analysis results for the three study regions

Region	Class	No. of axes retained	%Variation explained
Western Massachusetts	Forest	14	86.5
	Grassland	13	90.2
	Cropland	12	89.2
	High-density residential	12	90.4
	Low-density residential	10	81.2
	Urban	14	94.2
	Water	14	81.7
San Juan National Forest	Forest	15	92.2
	Open	15	86.7
	Riparian	14	82.6
	Water	14	89.2
Central Idaho	Forest	14	91.1
	Grassland	13	91
	Riparian	12	91.7
	Rock (barren)	12	77.7
	Shrubland	13	91

For each class in each region the table lists the number of axes retained based on the latent root criterion and the cumulative variance explained by those axes.

of the total variation of metrics across regions and cover classes.

Consistency is a measure of how consistent the meaning of a given landscape structural component is, when it is present. Each principal component is a dimension through a multi-dimensional space defined by the constituent metrics. A consistent landscape structural component is one that is oriented in nearly the same direction through this space for each region or cover class. We measured consistency as the average pair-wise Pearson's correlation among the factor patterns of the PC axes that are members of the same structural component group. For example, suppose that in the class-level analysis we found that a component predominantly related to edge contrast was present in 15 of the 16 cover classes across the three regions. We would quantify the consistency of this component by computing the average pair-wise correlations among the 120 combinations of the factor patterns of the component group. High average correlation of the factor patterns in a component group indicates that the landscape component is highly consistent in terms of how the different metrics contribute to it. Another way to think of consistency is that high average pair-wise correlation is a measure of how similarly the PCA components in that component group are oriented in the ''metric space''. We computed consistency scores over all regions at the landscape-level, and for all regions together at the class-level. In each case, we compared the average in-group pair-wise correlation of factor pattern to the average pair-wise correlation among all possible component combinations.

3. Results

3.1. *Class-level components*

For each of the seven landcover classes in western Massachusetts we retained 10–14 pPCA axes. These axes explained between 81.7% and 94.2% of the variance in the 49 class-level metrics, after accounting for the influences of PLAND (Tables 2 and 3). We retained 14 or 15 axes for each of the four landcover classes in the San Juan National Forest, which accounted for between 82.6% and 92.2% of the metric variance (Tables 2 and 3). In central Idaho we retained 12–14 axes for the five landcover classes, explaining 77.7–91.7% of the metric variance (Tables 2 and 3).

The cluster analysis of the full set of 211 retained pPCA axes resulted in a 24-cluster solution. Canonical DA indicated that the 24-cluster model was highly significant; not one of the 199 permutations reached a value as extreme as the sum of the observed canonical axes. In addition, the model explained >65% of the variance among groups, with canonical correlations for each of the first four axes well over 0.9. These results indicate that the 24 clusters identified are highly homogeneous and strongly distinguishable based on pPCA factor loadings. Partial canonical DA showed that there was no detectable effect of inter-regional differences on group discrimination. The partial model was as highly significant as the full model, also explained 65% of the variance among groups, and also had canonical correlations of the first four axes >0.9. Thus, the class-level differences among regions have no measurable effect on cluster homogeneity or separation. This finding is interesting because it implies that the landscape structure components identified in the clustering have a high degree of similarity across these three very different and geographically distinct study regions.

3.1.1. *Universality of class-level components*

Only one class-level landscape structure component, ''edge contrast'', was completely universal, occurring in all cover classes in all regions (Table 4). Another four components (''mean patch shape'', ''aggregation'', ''nearest neighbor distance'', and ''patch dispersion'') were nearly universal, being present in >85% of cover classes. Three more components (''large patch dominance'', ''neighborhood similarity'', and ''area–weighted correlation length and shape'') were present in >75% of cover classes (Table 4). In contrast, we

Table 3 – Meaning of 24 class-level configuration components identified through partial principal components analysis, clustering, and discriminant analysis

Component number	Component name	High loadings
1	Edge contrast	ECON_MN+ ECON_AM+ TECI+
2	Patch shape complexity	FRAC_MN+ SHAPE_MN+ FRAC_AM+ FRAC_MN+
3	Aggregation	AI+ PLADJ+ CLUMPY+ COHESION+
4	Nearest neighbor distance	ENN_MN+ ENN_AM+
5	Patch dispersion	ENN_CV+
6	Large patch dominance	LPI+ CORE_AM+ DCORE_AM+ AREA_AM+
7	Neighborhood similarity	SIMI_MN+ SIMI_AM+
8	Area–weighted proximity	PROX_AM+
9	Shape and correlation length of large patches	SHAPE_AM+ FRAC_AM+ GYRATE_AM+
10	Perimeter-area coefficient of variation	PARA_CV+
11	Patch size variability	AREA_CV+ CORE_CV+ DCORE_CV+
12	Proximity index coefficient of variation	PROX_CV+
13	Edge/patch density	ED+ LSI+ PD+ CWED+
14	Interspersion/juxtaposition	IJI+
15	Mean perimeter–area ratio	PARA_MN+
16	Splitting index	SPLIT+
17	Patch density	PD+
18	Mean patch size	AREA_MN+ CORE_MN+ GYRATE_MN+ DCORE_MN+
19	Edge contrast coefficient of variation	ECON_CV+
20	Edge + aggregation	ED+ CWED+ LSI+ AI− PLADJ− CLUMPY− FRAC_AM+
21	Split + cohesion	PLADJ− SPLIT+ COHESION−
22	Disjunct core area density	DCAD
23	Fractal dimension coefficient of variation	FRAC_CV
24	Area–weighted similarity	SIMI_AM

The components are listed in the order of the percentage of classes across regions (Table 4) containing that component. They are given a name based on the dominant factor loadings in the PCA. The metrics with the largest positive and negative loadings are listed.

identified five components that were present in only two of the 16 cover classes across the three regions. These infrequent components are not necessarily all ‘‘rare’’ dimensions of structure that are present only in a particular cover class in a particular study region. Rather, two of these five components (‘‘edge + aggregation’’ and ‘‘splitting index + cohesion’’ in Table 4) were components that in those particular cover classes combine two universal components. Edge density, splitting index, and aggregation are independent components in most cover classes in most regions, but are combined into complex components in a few cover classes. As a result, aggregation, like edge contrast, is a completely universal component of class-level landscape structure. All cover classes have either a pure or mixed component related to class-level aggregation metrics, such as aggregation index, percentage of like adjacencies, and clumpiness index (McGarigal et al., 2002). Likewise, ‘edge density’ and ‘splitting index’ are more universal than their raw scores indicate, with 62% and 56% of cover classes containing a pure or mixed edge or splitting component, respectively.

3.1.2. *Strength of class-level components*

Using the average eigenvalue and percent variance criteria, we found seven class-level landscape structure components (‘‘aggregation’’, ‘‘large patch dominance’’, ‘‘shape and correlation length of large patches’’, ‘‘patch size variation’’, ‘‘edge/patch density’’, ‘‘mean patch size’’, and ‘‘edge + aggregation’’) that were particularly strong. When present, each of these components explained on average >10% of the variance among the 49 class-level metrics (Table 4). Thus, these seven components are globally strongest across all cover classes and regions.

3.1.3. *Consistency of class-level components*

Most of the 24 class-level landscape structure components were highly consistent among cover classes and among regions based on average in-group pair-wise correlation of pPCA loadings (Table 4). The average in-group pair-wise correlation among factor loadings was 0.704, compared to the average correlation of all pair-wise combinations of 0.05. Fifteen of the 24 clusters had in-group correlation of factor scores >0.7, indicating remarkable consistency in the meaning of most components.

Table 4 – Universality, strength, and consistency of class-level landscape configuration components

No.	Component name	%MA	%CO	%ID	%Total	Average eigenvalue	%Variance explained	Average in-group correlation
1	Edge contrast	100	100	100	100	3.51	7.16	0.65
2	Patch shape complexity	86	100	80	94	3.34	6.39	0.72
3	Aggregation	86	75	100	88	6.44	11.50	0.79
4	Nearest neighbor distance	86	75	100	88	2.18	3.90	0.82
5	Patch dispersion	86	100	80	88	1.09	1.95	0.75
6	Large patch dominance	71	75	100	81	6.91	11.46	0.71
7	Neighborhood similarity	86	50	100	81	2.69	4.46	0.79
8	Area–weighted proximity	86	100	40	81	1.54	2.55	0.56
9	Shape and correlation length of large patches	71	75	80	75	5.43	8.31	0.74
10	Perimeter–area coefficient of variation	71	75	60	69	1.22	1.71	0.73
11	Patch size variability	86	25	60	63	4.67	5.96	0.72
12	Proximity index coefficient of variation	29	100	60	56	1.35	1.55	0.58
13	Edge/patch density	71	75	20	50	6.09	6.21	0.80
14	Interspersion/juxtaposition	57	50	40	50	1.29	1.32	0.68
15	Mean perimeter–area ratio	29	50	60	44	2.82	2.52	0.73
16	Splitting index	43	50	40	44	1.12	1.00	0.77
17	Patch density	14	75	40	38	2.11	1.61	0.57
18	Mean patch size	14	25	40	25	6.69	3.41	0.80
19	Edge contrast coefficient of variation	14	50	20	25	1.59	0.81	0.65
20	Edge + aggregation	14	25	0	13	8.47	2.16	0.82
21	Split + cohesion	14	25	0	13	3.32	0.85	0.72
22	Disjunct core area density	14	0	20	13	1.69	0.43	0.26
23	Fractal dimension coefficient of variation	14	0	20	13	1.63	0.42	0.73
24	Area–weighted similarity	0	50	0	13	1.54	0.39	0.81

Universality is measured as the percentage of the classes in each region (%MA, $N = 7$; %CO, $N = 4$; and %ID, $N = 5$) and across all classes and regions (%total, $N = 16$) containing the component. The average within-group eigenvalue and total variance explained quantify component strength. The average in-group pair-wise correlation of PCA factor loadings measure component consistency across classes and regions. The average of all in-group correlations across all classes, regions and components was 0.704. The average of all pair-wise correlations across all groups, classes, regions, and components was 0.052.

3.2. Landscape-level components

We retained between 10 and 14 principal components for the three landscape-level analyses corresponding to the three study areas. These components accounted for 88.2–94.1% of the total variance among the 54 landscape-level metrics (Tables 5 and 6). We clustered the 35 retained principal components across the three study regions and decided on a 17-cluster solution. The resulting DA model with 13 landscape metrics was highly significant based on Monte Carlo permutations ($p < 0.001$) and explained >64% of the variance among groups, with canonical correlations for each of the first four axes >0.99. These results indicate that the 17 clusters identified in the landscape-level analyses are highly homogeneous and strongly distinguishable based on PCA factor loadings. The partial DA model removing regional effects was as highly significant as the full model. Thus, at the landscape-level, as at the class-level, differences among regions have little effect on cluster homogeneity or separation.

3.2.1. Universality of landscape-level components

Eight landscape-level structure components were completely universal (i.e., were present in all three regions) and an equal number were present in only one of the three regions (Table 7). Unlike in the class-level analyses, none of these "rare" components were combinations of other more universal components. However, in several cases, components were separated into different clusters, even though they have the same interpretation based on the dominant factor loadings. For example, clusters 10 and 11 were both characterized by high mean radius of gyration and shape complexity, and clusters 13 and 15 were both characterized by high patch richness density. In these clusters, similarity in the dominant loadings was not enough to overcome differences in the loading structure across all metrics for these components.

3.2.2. Strength of landscape-level components

We found three landscape-level structure components that were particularly important. These three components had average eigenvalues >5 and explained, on average, >21% of the variance among the 54 landscape-level metrics, when present (Table 7). Two of these components ("contagion/diversity" and "large patch dominance") were substantially stronger than the others, explaining >21% and 33% of the variance, respectively. The dominance of these two components indicates more aspects of landscape structure are concentrated onto fewer axes at the landscape-level than the class-level.

3.2.3. Consistency of landscape-level components

Based on average in-group pair-wise correlation of PCA loadings, we found that all nine of the landscape-level structure components with more than a single group member had in-group correlations >0.6 (Table 7). In addition, the average in-group pair-wise correlation among factor loadings was 0.783, compared to the average of all pair-wise combina-

Table 5 – Summary of the landscape-level principal components analysis results among the three regions

Region	Number of axes	%Variation explained
Western Massachusetts	11	88.2
San Juan National Forest	14	94.1
Central Idaho	10	90.6

For each region, the table lists the number of axes retained based on the latent root criterion and the cumulative variance explained by those axes.

tions of 0.09. Indeed, in-group correlation of factor scores for five of the nine multi-member clusters were >0.8, indicating extreme consistency in the meaning of landscape-level structure components in terms of their orientation in metric space. It is interesting to note that the landscape-level clusters had substantially higher in-group consistency than those at the class-level.

4. Discussion

There are well over 100 statistical measures of landscape structure at both the class- and landscape-levels (McGarigal et al., 2002). It is critical to understand the theoretical and empirical relationships among these metrics so that informed decisions can be made regarding the choice of metrics for any particular application. Many of the metrics are theoretically related and many others are often empirically associated due to consistent coordination of different aspects of structure in real landscapes. It is therefore useful to quantify the redundancy of landscape metrics to identify a suite of structure components that together account for the major independent dimensions of landscape structure exhibited in real landscapes.

There are four major issues to address in attempts to describe the global redundancy of landscape metrics. First, it is essential to distinguish structure at the class-level from landscape-level. Studies at the class-level describe characteristics of patch size, shape, and neighborhood of focal cover class types and are typically used in the context of examining fragmentation effects. Landscape-level analyses examining spatial structure in multi-class patch mosaics provide information on overall landscape heterogeneity, texture, or graininess. Thus, it is likely that structure components at these two levels will differ. Previous studies have considered metrics at one level only (e.g., McGarigal and McComb, 1995) or combined metrics from both levels (e.g., Riitters et al., 1995, but see Linke and Franklin, 2006 and Schindler et al., 2008 for exceptions). Second, at the class-level it is especially important to distinguish between landscape composition and configuration because they are conceptually distinct aspects of landscape structure (Fahrig, 1997, 2002). Most metrics calculated for real landscapes confound different aspects of composition and configuration (Neel et al., 2004), yet there have been few attempts to quantitatively separate these effects (e.g., McGarigal and McComb, 1995; Villard et al., 1999). The third major issue involves what metrics to include in the analysis. The patterns of metric redundancy observed are

Table 6 – Meaning of landscape-level configuration components identified through principal components analysis, clustering, and discriminant analysis

Component number	Component name	High loadings
1	Contagion/diversity	AI+ PLADJ+ CONTAG+ CAI_AM+ ED− CWED− LSI− PARA_AM− DCAD− SIDI− SIEI−
2	Large patch dominance	LPI+ AREA_CV+ CORE_CV+ GYRATE_AM+ COHESION+ DIVISION− SPLIT−
3	Interspersion/juxtaposition	IJI+
4	Edge contrast	ECON_MN+ ECON_AM+ TECI+
5	Patch shape variability	SHAPE_CV+ FRAC_CV+
6	Mean proximity	PROX_MN+
7	Nearest neighbor distance	ENN_AM+
8	Patch dispersion	ENN_CV+
9	Area–weighted proximity	PROX_AM+
10	Patch shape and gyration 1	SHAPE_MN+ FRAC_MN+ GYRATE_MN+
11	Patch Shape and gyration2	SHAPE_MN+ FRAC_MN+ GYRATE_MN+
12	Core area	CAI_MN+ CAI_CV−
13	Patch richness density	PRD+
14	Mean perimeter–area ratio	PARA_MN+
15	Patch richness density	PRD+
16	Perimeter–area ratio variation	PARA_CV+
17	Mean nearest neighbor distance	ENN_MN+

The components are listed in the order of the percentage of regions (N = 3) containing that component. They are given a name based on the dominant factor loadings in the PCA. Metrics with the largest positive and negative loadings are listed.

directly a result of which metrics are calculated. For example, including several metrics that exhibit similar behavior will necessarily increase redundancy. Likewise, failure to include metrics from behaviorally distinct groups will result in reduced dimensionality of measured landscape structure. Fourth, it is necessary to separately evaluate different aspects

Table 7 – Universality, strength, and consistency of landscape-level structure components					
Component number	Component name	%Total	Average eigenvalue	%Variance explained	Average in-group correlation
1	Contagion/diversity	100	18.10	33.52	0.92
2	Large patch dominance	100	11.36	21.04	0.84
3	Interspersion/juxtaposition	100	5.80	10.74	0.6
4	Edge contrast	100	2.95	5.55	0.6
5	Patch shape variation	100	2.32	4.29	0.73
6	Mean proximity	100	1.36	2.51	0.89
7	Nearest neighbor distance	100	1.14	2.1	0.84
8	Patch dispersion	100	1.04	1.93	0.86
9	Area–weighted proximity	67	1.32	1.62	0.77
10	Patch shape and gyration 1	33	9.37	5.78	na
11	Patch shape and gyration 2	33	5.59	3.45	na
12	Core area	33	2.11	1.3	na
13	Patch richness density	33	1.99	1.22	na
14	Mean perimeter–area ratio	33	1.57	0.97	na
15	Patch richness density	33	1.56	0.96	na
16	Perimeter–area ratio variation	33	1.39	0.86	na
17	Mean nearest neighbor distance	33	1.31	0.81	na

The percentage of regions (%total, $N = 3$) containing the component is a measure of component universality. The average in-group eigenvalue and total variance explained are measures of component strength. The average in-group pair-wise correlation of PCA factor loadings is a measure of component consistency across regions. The average of all in-group correlations across all regions and components was 0.783. The average of all pair-wise correlations across all regions and components was 0.094.

of coordination and redundancy of metrics across many landscapes. We have used a hierarchical analysis to describe three measures (universality, strength, and consistency) for this evaluation. When a single analysis combines the structure components from hundreds of landscapes across a single large region, it is not possible to separately measure the consistency or universality of the identified components. Thus, such an analysis cannot separate universality and consistency from component strength. The only way to separate these three important aspects of structural component coordination is to conduct a replicated, hierarchical analysis.

4.1. *Component universality, strength, and consistency*

Prior to examining the important structure components in detail, a short discussion of the broader interpretation of our measures of component importance is warranted. Of our three measures, universality may be the most relevant assessment of importance because it provides a measure of how globally present the component is across the replicate regions and cover classes. Universal structure components are more likely to reflect inherent and independent attributes that have important implications for understanding the nature of landscape structure and its relations to ecological processes.

Consistency provides a measure of how similar groups of structure components are, in terms of their orientation in metric space. Highly consistent components are those that are projected in parallel with respect to the metrics that comprise them, and thus measure the same aspect of landscape structure. Thus, while universality tells how globally present a component is, consistency tells us how stable a component is in terms of the behavior of its constituent metrics. In other words, consistency measures the variability of the meaning of the structure component. Thus, component groups with high levels of consistency allow more precise ecological interpretation. Consistent components also provide more confidence that we can reliably represent those components with subsets of metrics.

Strength measures the total amount of variance explained by a component. A landscape structure component identified by PCA or pPCA is "strong" if it captures a relatively large percentage of the variance among the metrics included in the analysis. While variance explained is an intuitively appealing measure of importance, component strength is primarily related to the number of metrics that load highly onto that component and is also likely related to the chosen data reduction technique (e.g., PCA). Thus, "strength" quantifies the coordination and redundancy of the metrics included in the chosen analysis. Because we did no variable reduction prior to our PCA, we included many highly redundant metrics that necessarily load onto the same component, potentially making it appear very important. Had we removed correlated variables prior to analysis, the relative component strengths would have been quite different. Component strength is helpful in identifying the number of independent structure components that can be measured by the full suite of available metrics and for identifying the degree to which individual metrics are redundant with one another. However, component strength has little additional utility because the degree to which multiple landscape metrics measure aspects of the same underlying structure component does not necessarily provide any information about the ecological importance of a component in relation to any organism or process of interest.

The strength, universality, and consistency of landscape structure components are different things, and should be conceptualized and analyzed separately. Indeed, in both our class- and landscape-level analyses there were no significant correlations between component strength, and either component universality or consistency.

Table 8 – Seven highly universal and consistent class-level landscape structure components across many different cover classes in 531 landscapes across three very different and disjunct regions of North America based on the results in Table 3

Component name	Description
Edge contrast	Degree of "contrast" between the focal class and its neighborhood, where contrast is user-defined and represents the magnitude of difference between classes in one or more attributes.
Patch shape complexity	Shape complexity of patches of the focal class, where shape is defined by perimeter–area relationships.
Aggregation	Degree of aggregation of cells of the focal class, where large, compact clusters of cells of the focal class are considered to be aggregated.
Nearest neighbor distance	Proximity of patches of the focal class, based on the average or area–weighted average distance between nearest neighbors.
Patch dispersion	Spatial dispersion of patches across the landscape, reflecting whether patches of the focal class tend to be uniformly distributed or overdispersed (clumped) based on variability in nearest neighbor distances.
Large patch dominance	Degree of concentration of focal class area in few, large patches with large core areas.
Neighborhood similarity	Degree of isolation of patches from nearby patches of the same or similar class (i.e., degree of similarity of the neighborhood surrounding patches of the focal class in terms of patch composition).

4.2. *Components of landscape structure*

Our results suggest that there are a number of universal and highly consistent components of landscape structure at the class-level. These major components and their interpretations are described in Table 8 and are based on the results in Table 3. The importance of finding seven highly universal and consistent structure components is underscored by dramatic variation in the cover classes included in the analysis from forest, to grassland, to urban development, to water and riparian strips, and by the fact that the three regions did not share a common landcover classification scheme. Given that these cover class types are constrained by very different geomorphic and ecological factors, there was no reason a priori to expect that we would find any components that were universally important and highly consistent. Two of these components, patch shape complexity and edge contrast, were also identified as being important by McGarigal and McComb (1995); however in that study they were combined into one component rather than being two independent components.

At the landscape-level nearly half of the independent landscape structure components we identified were completely universal across the three regions, and all of these were highly consistent (Tables 9 and 6). Overall, the structure components at the landscape-level appeared to be generally more consistent in their meaning, and perhaps more universal, than those at the class-level. However, the large difference in the size of the clusters between the class-level and landscape-level makes this comparison equivocal. It is also worth noting that five structure components were important at both the cover class- and landscape-level (large patch dominance, edge contrast, aggregation/contagion, nearest neighbor distance, and patch dispersion).

Other than our "contagion/diversity" component, which is comparable to their "image texture" component, there is little concordance between these components and the six components identified by Riitters et al. (1995). Some of the discrepancies are due to differences in the metrics included in each study. For example, in our analysis interspersion and juxtaposition (IJI), edge contrast, and patch shape variability

Table 9 – Seven universal landscape structure components derived from 531 landscapes across three very different and disjunct regions of North America based on the results in Table 6

Component name	Description
Contagion/diversity	Degree of aggregation of patch types (or the overall clumpiness of the landscape) and the diversity/evenness of patch types. Contagion and diversity are inversely related; clumped landscapes containing large, compact patches and an uneven distribution of area among patch types have high contagion and low diversity.
Large patch dominance	Degree of landscape dominance by large patches.
Interspersion/juxtaposition	Degree of intermixing of patch types.
Edge contrast	Degree of "contrast" among patches, where contrast is user-defined and represents the magnitude of difference between classes in one or more attributes.
Patch shape variability	Variability in patch shape complexity, where shape is defined by perimeter–area relationships.
Proximity	Degree of isolation of patches from nearby patches of the same class.
Nearest neighbor distance	Proximity of patches to neighbors of the same class, based on the area–weighted average distance between nearest neighbors.

represent three independent components based on metrics that were not included in the Riitters et al. (1995) study. There are also discrepancies that are potentially due to differences in scales of the two analyses. Riitters et al. (1995) sampled 85 large landscapes to represent the different physiographic regions of the United States and all landscapes were included in the factor analysis. Their individual landscapes were roughly comparable in size to each of the regions from which we subsampled landscapes. Thus, they sampled more coarsely across longer gradients of landscape structure. Because pattern-generating processes vary so much between physiographic regions, it is likely more relevant to examine structure within regions when the goal is to relate pattern and process, or to relate pattern to the ecology of a particular organism of interest.

Number of attribute classes (patch richness) was also important in Riitters et al. (1995) and was a component in two of our regions, but again these components were sufficiently different from one another to be clustered separately thus they have low universality (components 13 and 15, Table 6). The difference in importance of patch richness is most likely due to differences in number of classes between the studies (4–7 in ours versus 37 in theirs) in addition to the effects of sampling shorter gradients discussed above.

Linke and Franklin (2006) have repeated the class-level analysis presented here on an independent study area in Alberta, Canada. Their analysis is thus an independent evaluation of the universality and consistency of the components of landscape structure that we identified in an entirely different ecological system. They identified 20 clusters, 15 of which are very similar to the ones reported here at the class-level. These 15 gradients included all seven parsimonious structure gradients, with five being nearly universal and consistent. Linke and Franklin's (2006) results are highly concordant with those presented here and suggest that the patterns of universality, consistency, and importance we identify may be general properties of landscape mosaics and not idiosyncratic to the particular study areas that we have tested.

5. Conclusions

Our study resulted in several major findings. First, metric redundancy (component strength), universality, and consistency of landscape structure components are different things, and must be conceptualized and analyzed separately. Components in which many metrics participate are not necessarily any more or less universal or consistent across regions or cover classes than those with fewer metrics.

Component strength did, however, demonstrate that there is considerable redundancy among both class- and landscape-level metrics, as a number of other studies have found. We were able to reduce 49 class-level and 54 landscape-level metrics to 24 independent class-level components and 17 independent landscape-level components. While this is a considerable reduction in the dimensionality, it is far less than that reported by previous studies (McGarigal and McComb, 1995; Riitters et al., 1995). The fact that we found substantially less total redundancy among the landscape metrics we calculated at both the class- and landscape-levels than the earlier studies may reflect the fact that we computed a number of new metrics that quantify different aspects of landscape structure that were not included in the earlier analyses. Using these new metrics resulted in a number of new dimensions of independent structure that had not been described before including ''patch dispersion'', ''similarity'', ''area–weighted mean proximity index'', ''variability in shape complexity'', and ''correlation length'' among others. Clearly the choice of metrics to be analyzed has a major influence on the observed redundancy and dimensionality of landscape structure.

Second, there was remarkable universality and consistency of many of the components we identified at both the class- and landscape-levels. A fairly large number of class- and landscape-level structure components are both highly universal and highly consistent. These dimensions are likely to be inherent properties of patchiness measured with the metrics we used, and are likely to be present and have the same general meaning in most landscapes. However, there were an equal number of independent landscape structure components identified at both the class- and landscape-levels that had low universality. In most cases, components that had low universality were unique dimensions of structure that were not present in the majority of cover classes or regions. This is not surprising, as one would expect that there would be some dimensions of landscape structure that emerge under certain conditions, and that these conditions would not necessarily be present in all cover classes or regions. Thus, there seem to be both universal and idiosyncratic components of landscape structure at the class- and landscape-levels. This is supported by the independent evaluation produced by Linke and Franklin (2006).

We suggest that the components we identified as being highly universal and consistent form a minimum set of structure attributes necessary to characterize in studies seeking to describe structure patterns within particular landscapes. Further, only one or a few metrics within each group need to be quantified since they are highly redundant. Choice of particular metrics would of course also be based on the research questions being addressed and on known metric behavior (e.g., Neel et al., 2004). We need to emphasize, however, that our list of universal and strong components would not be sufficient to capture the full suite of dimensions in every study area. Rather, it is likely that in other landscapes and other regions our universal components will be present and will consistently be represented by the constituent metrics, but that other unique components may also be present. A priori there is no way to determine if and how many rare, or unique dimensions of landscape structure may exist.

Finally, it is important to remember that our measures of universality, strength, and consistency refer only to the components of structure as measured by landscape structure metrics. They have no inherent connection as such to any organism or process responses. It is ultimately essential to interpret the meaning of landscape structure components with respect to the response of some organism or process of interest (Tischendorf, 2001). In this paper our interest was primarily to describe universal and consistent patterns in objective landscape structure metrics. However, our approach could easily be adapted to explicitly relate patterns with processes. One could use nonlinear regression, canonical correspondence analysis (CCA), redundancy analysis (RDA), or classification and regression trees (CART) (Breiman et al., 1984; ter Braak, 1986; Steinberg and Colla, 1997), for example, to extract components of landscape structure that are explicitly related to a response variable, or sets of response variables. In that context, component strength would provide a measure of the power of the component to predict the response variable(s). Likewise, universality and consistency in that context would reflect the dimensions of landscape structure that were universally and consistently related to the response variable(s). Ideally, one would conduct both sets of analyses, one relating pattern and process, and one describing the major components of structure. Results of these analyses would elucidate the differences between what we map and measure and how the processes we are studying respond to those patterns.

Acknowledgments

Funding for this work was provided in part by a United States Department of Education GAANN program graduate fellowship to SAC and a David H. Smith Conservation Research Fellowship to MCN. This material is based on work partially supported by the Cooperative State Research, Extension, Education Service, U.S. Department of Agriculture, Massachusetts Agricultural Experiment Station and the Department of Natural Resources Conservation, under Project No. 3321 of The Nature Conservancy's David H. Smith Conservation Research Fellowship Program.

REFERENCES

Baker, W.L., Cai, Y., 1992. The r.le programs for multiscale analysis of landscape structure using the GRASS geographical information system. Landscape Ecol. 7, 291–302.

Baldwin, D.J.B., Weaver, K., Schnekenburger, F., Perera, A.H., 2001. Sensitivity of landscape pattern indices to spatial extent, data resolution, and classification detail in the managed forest of Ontario. Forest Research Report No. 150, Ontario Ministry of Natural Resources, Sault Ste. Marie, Ontario, Canada, p. 45.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Chapman and Hall/CRC, Boca Raton, FL, USA.

Cain, D.H., Riitters, K., Orvis, K., 1997. A multi-scale analysis of landscape statistics. Landscape Ecol. 12, 199–212.

Cifaldi, R.L., Allan, J.D., Duh, J.D., Brown, D.G., 2004. Spatial patterns in land cover of exurbanizing watersheds in southeastern Michigan. Landscape Urban Plan 66, 107–123.

Fahrig, L., 2002. Effects of habitat fragmentation on the extinction threshold: a synthesis. Ecol. Appl. 12, 346–353.

Fahrig, L., 1997. Relative effects of habitat loss and fragmentation on population extinction. J. Wildlife Manag. 61, 603–610.

Griffith, J.A., Martinko, E.A., Price, K.P., 2000. Landscape structure analyses of Kansas in three scales. Landscape Urban Plan 52, 45–61.

Gustafson, E.J., 1998. Quantifying landscape spatial pattern: what is the state of the art? Ecosystems 1, 143–156.

Gustafson, E.J., Parker, G.R., 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecol. 7, 101–110.

Hargis, C.D., Bissonette, J.A., David, J.L., 1998. The behavior of landscape metrics commonly used in the study of habitat fragmentation. Landscape Ecol. 13, 167–186.

He, H.S., DeZonia, B.E., Mladenoff, D.J., 2000. An aggregation index (AI) to quantify spatial patterns of landscapes. Landscape Ecol. 15, 591–601.

Jaeger, J.A.G., 2000. Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landscape Ecol. 15, 115–130.

Lausch, A., Herzog, F., 2002. Applicability of landscape metrics for the monitoring of landscape change: issues of scale, resolution and interpretability. Ecol. Indicators 2, 3–15.

Li, H., Reynolds, J.F., 1995. On definition and quantification of heterogeneity. Oikos 73, 280–284.

Linke, J., Franklin, S.E., 2006. Interpretation of landscape structure gradients based on satellite image classification of land cover. Canadian Journal of Remote Sensing. 32 (6), 367–379.

McGarigal, K., 2002. Landscape pattern metrics. In: El-Shaarawi, A.H., Piegorsch, W.W. (Eds.), Encyclopedia of Environmetrics, 2. John Wiley & Sons, Chichester, England, pp. 1135–1142.

McGarigal, K., Cushman, S.A., Stafford, S., 2000. Multivariate Statistics for Wildlife and Ecology Research. Springer, New York, USA.

McGarigal, K., Marks, B.J., 1995. FRAGSTATS: Spatial Analysis Program for Quantifying Landscape Structure. USDA Forest Service General Technical Report PNW-GTR-351.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, available at the following web site: http://www.umass.edu/landeco/research/fragstats/fragstats.html.

McGarigal, K., McComb, W.C., 1995. Relationships between landscape structure and breeding birds in the Oregon Coast range. Ecol. Monographs 65, 235–260.

Neel, M.C., McGarigal, K., Cushman, S.A., 2004. Behavior of class-level landscape metrics across gradients of class aggregation and area. Landscape Ecol. 19, 435–455.

O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H., Graham, R.L., 1988. Indices of landscape pattern. Landscape Ecol. 1, 153–162.

Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P., Jones, K.B., Jackson, B.L., 1995. A factor analysis of landscape pattern and structure metrics. Landscape Ecol. 10, 23–40.

SAS, 2002. SAS System. SAS Institute, Cary, North Carolina, USA.

Scanes, H.M., Bunce, R.G.H., 1997. Directions of landscape change (1741–1993) in Virestad, Sweden—characterized by multivariate analysis. Landscape Urban Plan 38, 61–75.

Schindler, S., Poirazidis, K., Wrbka, T., 2008. Towards a core set of landscape metrics for biodiversity assessments: A case study from Dadia National Park. Greece. Ecol. Indicators 8, 502–514.

Steinberg, D., Colla, P., 1997. CART—Classification and Regression Trees. Salford Systems. San Diego, CA, USA.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: A new eigenvector technique for multivariate direct gradient analysis. Ecology 67 (5), 1167–1179.

ter Braak, C.J.F., Šmilauer, P., 1998. CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4). Microcomputer Power, Ithaca, NY, USA.

Tinker, D.B., Resor, C.A.C., Beauvais, G.P., Kipfmueller, K.F., Fernanades, C.I., Baker, W.L., 1998. Watershed analysis of

forest fragmentation by clearcuts and roads in a Wyoming forest. Landscape Ecol. 13, 149–165.
Tischendorf, L., 2001. Can landscape indices predict ecological processes consistently? Landscape Ecol. 16, 235–254.
Turner, M.G., 1990. Spatial and temporal analysis of landscape patterns. Landscape Ecol. 4, 21–30.
Turner, M.G., Gardner, R.H., 1991. Quantitative Methods in Landscape Ecology. Springer-Verlag, New York, USA.
Villard, M.-A., Trzcinski, M.K., Merriam, G., 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conservation Biol. 13, 774–783.