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Original Article

Towards more predictable and consistent landscape metrics across spatial scales

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ABSTRACT

Habitat change and fragmentation are considered key drivers of environmental change and biodiversity loss. To understand and mitigate the effects of such spatial disturbances on biological systems, it is critical to quantify changes in landscape pattern. However, the characterization of spatial patterns remains complicated in part because most widely used landscape metrics vary with the amount of usable habitat available in the landscape, and vary with the scale of the spatial data used to calculate them. In this study, we investigate the nature of the relationship between intrinsic characteristics of spatial pattern and extrinsic scale-dependent factors that affect the characterization of landscape patterns. To do so, we used techniques from modern multivariate statistics to disentangle widely used landscape metrics with respect to four landscape components: extent (E), resolution (R), percentage of suitable habitat cover (P), and spatial autocorrelation level (H). Our results highlight those metrics that are less sensitive to change in spatial scale and those that are less correlated. We found, however, significant and complex interactions between intrinsic and extrinsic characteristics of landscape patterns that will always complicate researcher's ability to isolate purely landscape pattern driven effects from the effects of changing spatial scale. As such, our study illustrates the need for a more systematic investigation of the relationship between intrinsic characteristics and extrinsic properties to accurately characterize observed landscape patterns.

1. Introduction

Landscape pattern refers to discrete landscape features of an ecosystem (composition) and their spatial arrangement (configuration) within the landscape. Biotic and abiotic determinants, as well as human activities, have been shown as driving forces that shape landscape patterns (Turner, 1990). Furthermore, the rate, extent and magnitude of human alteration of the earth's terrestrial surface is greater now than ever in history, driving unprecedented change in ecosystem processes (Lambin et al., 2001). Such changes range from biodiversity loss and climate change to important modification of ecosystem services (Foley et al., 2005). Accurately quantifying and characterizing landscape pattern has therefore become a major priority for addressing a wide range of spatial analysis applications (Turner, 2005).

In this regard, a plethora of quantitative metrics have been developed to ostensibly provide simple quantitative measurements of the composition and configuration of a landscape (Baker and Cai, 1992; McGarigal and Marks, 1995; O'Neill et al., 1988; Turner, 1990). In general, the calculation of these landscape metrics requires the use of a categorical map, often indicating land-cover or land-use. Typically, these metrics are then used to investigate the relationship between landscape pattern and ecological processes, or as an indicator of ecological condition and risk (O'Neill et al., 1997; Uuemaa et al., 2013). They are also of key importance for identifying or detecting critical spatial and temporal changes in landscape patterns to anticipate abrupt ecological transition (Johnson and Patil, 2007). The outcome of such spatial analyses, however, remains limited by constraints in our ability to quantify the changes in landscape pattern (Turner, 2005; Uuemaa et al., 2013). In particular, the characterization of landscape patterns depends not only on the patterns themselves but also on the way they are represented (Wu, 2013).

Multiple scale-dependent factors can affect the characterization of a landscape pattern. For example, most landscape metrics are sensitive to changes in the resolution (grain size) of the spatial data (Frohn and Hao, 2006; He et al., 2000; Li et al., 2005; Saura, 2004; Wickham and Rhtters, 1995; Wu, 2004), the extent of

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the area under investigation (Frohn and Hao, 2006; Li et al., 2005; Saura and Martinez-Millan, 2001; Szab et al., 2014; Wu, 2004; Wu et al., 2002), or the classification scheme of categorical maps (Bailey et al., 2007; Buyantuyev and Wu, 2007; Castilla et al., 2009; Li et al., 2005; Peng et al., 2010). There are many examples of studies that have investigated the sensitivity of landscape metrics to change in spatial scales (Saura and Martinez-Millan, 2001; Wu, 2004; Wu et al., 2002). Such studies typically target a small set of landscape metrics and base conclusions about the effect of spatial scale on landscape metrics on unique case studies, investigating a single or two scale-dependent factors in isolation (Lechner et al., 2013). Thus far, limited consideration has been given to the vexing question of interaction between scale dependent-factors and change in the landscape patterns (Lechner et al., 2013; Peng et al., 2010).

Additionally, the use and application of landscape metrics is hampered by several characteristics of the metrics themselves (Uuemaa et al., 2013). Many landscape metrics are strongly correlated with the proportion of habitat cover on the landscape (Neel et al., 2004). As a consequence, metrics used to characterize particular aspects of the configuration of the landscape pattern cannot be easily interpreted if the proportion of habitat cover on the landscape is different (Neel et al., 2004; Remmel and Csillag, 2003; Wang and Cumming, 2011). Furthermore, no single metric can fully capture and describe intricate landscape pattern. On the other hand, reducing the number of metrics by correlation and ordination techniques has failed to render the ecological meaning of the latent metric to the practitioner (Turner, 2005). Several suggestions have been made for a minimum set of metrics that capture independent elements of the variation in observed landscape patterns while minimizing redundancy and capturing the desired qualities (Riitters et al., 1995; Cushman et al., 2008). Nonetheless, no general framework exists that permits a particular component of landscape patterns to be unambiguously linked to specific landscape metrics.

To address these persistent challenges, most previous research has been directed toward developing a more rigorous statistical interpretation of landscape metrics. The development of the neutral landscape model (Gardner et al., 1987; With et al., 1997) has provided a framework for generating replicated landscape patterns with partially controllable spatial properties, particularly with respect to their composition and configuration of components (Turner, 2005). Inspection of the relationships among landscape metrics revealed that many were nonlinear and often not monotonic across composition and configuration scenarios (Neel et al., 2004; Remmel and Csillag, 2003). However, most of these studies were limited to maps of the same spatial extent and resolution to avoid the confounding effects of these extrinsic scale-dependent factors. There is dearth of studies that explicitly assess the relative importance of scale-dependent factors versus changes in intrinsic characteristics of landscape patterns on the characterization of spatial patterns (Estreguil et al., 2014; Lechner et al., 2013). Yet, it is critical to determine whether a change in spatial scale has the same effect in all spatial patterns or whether particular types of spatial patterns (e.g. those with high fragmentation level) are more sensitive to a change in spatial scale than others.

The primary aim of this study was to investigate the nature of the relationship between intrinsic characteristics of spatial patterns and extrinsic scale-dependent factors that affect the characterization of landscape patterns. This research is motivated by the need to identify a set of key generic landscape metrics that enable concise characterization of independent aspects of spatial patterns regardless of the scale at which the patterns are represented (Lindenmayer et al., 2008). In terms of scale-dependent factors affecting the representation of landscape patterns, we investigated the role of spatial resolution (R) and spatial extent (E). These scale-dependent factors were tested in relation to the intrinsic characteristics of the landscape patterns themselves as described by the spatial autocorrelation (H) and the percentage of suitable habitat cover (P). We first tested the statistical significance of the interaction between landscape pattern and scale-dependent factors to assess the magnitude of these interactions and their statistical effect on landscape metrics. Second, we showed how a self-organizing map (SOM) can be used to identify less correlated subsets of landscape metrics thereby providing a robust alternative to traditional ordination techniques.

Table 1
List of predictor variables tested and values.

Predictor variables	Measures
Intrinsic characteristic	
Landscape spatial autocorrelation (Fragmentation)	H = 0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1
Percentage of suitable habitat cover in a binary scheme	P = 5, 15, 25, 35, 45, 55, 65, 75, 85, 95%
Scale-dependent factor	
Spatial extent	E = 640, 1280, 2560 m^2
Spatial resolution or pixel size	R = 10, 20, 40 m

2. Materials and methods

2.1. Landscape patterns and landscape metrics generation

We used the computer program Qrule 4.2 to generate a wide range of landscape patterns, in which fragmentation (measured as the degree of spatial autocorrelation) and proportion of habitat cover can be systematically and independently controlled (Gardner, 1999; Gardner and Urban, 2007). We considered a binary distinction between suitable and unsuitable habitat type. Qrule uses a midpoint displacement algorithm (Saupe, 1988) to generate multi-fractal maps in which the degree of spatial autocorrelation among adjacent cells (H) can be controlled. We generated landscape patterns in a full factorial design across an 11-step gradient in spatial autocorrelation (H = 0–1 in increments of 0.1, 0 being close to random and 1 being completely clustered) and a 10-step gradient in proportion of suitable habitat habitat cover (P = 5–95% in 10% increments) with 100 replicate landscapes for each of the 110 factor combinations (Table 1). In order to analyse the influence of spatial extent and resolution on landscape metrics, we generated binary landscape patterns for 40, 20 and 10 m cell size raster and three different extents of 640×640, 1280×1280, and 2560×2560 m^2 (Table 1). We used independent realizations for each spatial scale to assure the statistical independence of the estimates corresponding to different resolution and extent.

For each sample landscape, we calculated 101 landscape metrics using the computer program FRAGSTATS 4.2 (McGarigal et al., 2012). The metrics were defined for the suitable habitat cover only and are commonly referred as class-level metrics. McGarigal et al. (2012) categorized these metrics into five groups corresponding to the aspect of landscape structure emphasized. These include area/edge/density, shape, core area, contrast and aggregation (Table 2). Metric calculation was based on a 80 m edge depth affecting metrics related to core area, a 400 m search radius affecting metrics based on the distribution of suitable habitat cells within a specified distance of a focal point and an eight-neighbour rule.

2.2. Permutational multivariate analysis of variance

To test the null hypothesis of no statistical difference between landscape metrics for four predictor variables, spatial extent (E), spatial resolution (R), percentage of suitable habitat cover (P), and spatial aggregation (H), we used the permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). This

Table 2
List of response variables tested and ranges. A detailed description of each metric can be found in McGarigal et al. (2012). Twelve metrics characterize the aggregation properties of the patches (cells) belonging to the suitable area only. The first- and second-order statistics are as following: mean (MN), area-weighted mean (AM), median (MD), range (RA), standard deviation (SD), and coefficient of variation (CV).

Response variables	Measures	Range
Area/density/edge metrics		
Total suitable area	CA/TA (ha)	1.78–624.03
Percentage of Landscape	PLAND (ha)	4.34–96.01
Number of patches	NP	1.0–1355.4
Patch density	PD	0.24–256.45
Total edge	TE (m)	750.00–31.55 $\times 10^4$
Edge density	ED (m/ha)	3.76–540.04
Landscape shape index	LSI	1.22–49.19
Normalized Landscape shape index	nLSI	0.01–0.75
Largest patch index	LPI (%)	0.62–95.98
Patch area distribution	AREA_MN(ha)	0.03–492.58
	AREA_AM (ha)	0.18–623.65
	AREA_MD(ha)	0.01–467.98
	AREA_RA(ha)	0.00–622.48
	AREA_SD (ha)	0.00–243.01
	AREA_CV (ha)	0.00–2243.21
Radius of gyration distribution	GYRATE_MN(ha)	6.93–769.62
	GYRATE_AM (ha)	17.55–976.70
	GYRATE_MD (ha)	5.00–732.29
	GYRATE_RA (ha)	0.00–972.27
	GYRATE_SD (ha)	0.00–372.62
	GYRATE_CV (ha)	0.00–587.09
Shape metrics		
Perimeter-area ratio distribution	PARA_MN	79.36–3613.27
	PARA_AM	21.55–2741.45
	PARA_MD	79.36–4000.00
	PARA_RA	0.00–3972.13
	PARA_SD	0.00–1521.89
	PARA_CV	0.00–65.28
Shape index distribution	SHAPE_MN	1.09–2.90
	SHAPE_AM	1.18–28.58
	SHAPE_MD	1.00–2.74
	SHAPE_RA	0.00–30.24
	SHAPE_SD	0.00–1.94
	SHAPE_CV	0.00–131.17
Fractal index distribution	FRAC_MN	1.02–1.15
	FRAC_AM	1.03–1.43
	FRAC_MD	1.00–1.14
	FRAC_RA	0.00–0.46
	FRAC_SD	0.00–0.10
	FRAC_CV	0.00–9.19
Related circumscribing circle distribution	CIRCLE_MN	0.19–0.47
	CIRCLE_AM	0.38–0.71
	CIRCLE_MD	0.00–0.49
	CIRCLE_RA	0.00–0.87
	CIRCLE_SD	0.00–0.32
	CIRCLE_CV	0.00–151.29
Contiguity index distribution	CONTIG_MN	0.08–0.90
	CONTIG_AM	0.16–0.99
	CONTIG_MD	0.00–0.90
	CONTIG_RA	0.00–0.99
	CONTIG_SD	0.00–0.38
	CONTIG_CV	0.00–195.36
Core metrics		
Total core area	TCA	0.00–531.55
Core area percentage of landscape	CPLAND (%)	0.00–81.11
Number of disjunct core areas	NDCA	0.00–35.97
Disjunct core area density	DCAD	0.00–531.12
Core area distribution	CORE_MN (ha)	0.00–420.04
	CORE_AM (ha)	0.00–531.41
	CORE_MD (ha)	0.00–399.31
	CORE_RA (ha)	0.00–511.58
	CORE_SD (ha)	0.00–198.35
	CORE_CV (ha)	0.00–2869.97
Disjunct core area distribution	DCORE_MN (ha)	0.00–488.24
	DCORE_AM (ha)	0.00–531.12
	DCORE_MD (ha)	0.00–482.21
	DCORE_RA (ha)	0.00–421.25
	DCORE_SD (ha)	0.00–180.97
	DCORE_CV (ha)	0.00–374.41
Core area index distribution	CAI_MN (%)	0.00–67.33
	CAI_AM (%)	0.00–85.18
	CAI_MD (%)	0.00–66.02
	CAI_RA (%)	0.00–82.18
	CAI_SD (%)	0.00–31.90
	CAI_CV (%)	0.00–2858.56
Aggregation metrics		
Percentage of like adjacencies	PLADJ (%)	17.88–99.41
Clumpiness index	CLUMPY	0.18–0.98
Aggregation index	AI (%)	25.46–99.81
Landscape division index	DIVISION (proportion)	0.08–10.99
Splitting index	SPLIT	1.09–21343.27
Effective mesh size	MESH (ha)	0.01–593.82
Patch cohesion index	COHESION	34.21–99.98
Connectance index	CONNECT (%)	0.00–88.76
Proximity index distribution	PROX_MN	0.00–12,476.31
	PROX_AM	0.00–1255.84
	PROX_MD	0.00–1255.85
	PROX_RA	0.00–14,864.24
	PROX_SD	0.00–15,553.64
	PROX_CV	0.00–5743.96
Similarity index distribution	SIMI_MN	0.00–12,476.31
	SIMI_AM	0.00–1255.84
	SIMI_MD	0.00–1255.85
	SIMI_RA	0.00–14,864.24
	SIMI_SD	0.00–15,553.64
	SIMI_CV	0.00–5743.96
Contrast metrics		
Contrast-weighted edge density	CWED (m/ha)	6.76–540.04
Total edge contrast index	TECI (%)	23.31–99.01
Edge contrast index distribution	ECON_MN (%)	23.31–99.25
	ECON_AM (%)	23.31–98.80
	ECON_MD (%)	32.31–100.00
	ECON_RA (%)	0.00–57.71
	ECON_SD (%)	0.00–23.01
	ECON_CV (%)	0.00–28.14

method provides an alternative to traditional analysis of variance (ANOVA/MANOVA) that is distribution free and insensitive to the correlation among response variables (in our case, landscape metrics). PERMANOVA involves the construction of a distance matrix which reflects the similarity/dissimilarity of each pair of simulated landscape patterns with respect to their landscape metric values (Anderson, 2001). The PERMANOVA analysis is then based on partitioning the multivariate variation of the distance measures. We standardized landscape metric values and used Euclidean distances to model the relationships among simulated landscape patterns. The final test statistic is a multivariate analogue to the traditional parametric univariate Fishers F-ratio (Anderson, 2001). However, the hypothesis (H_0) of no difference among a priori defined groups of landscapes is evaluated using a Fishers F-test based on sequential sums of squares from 999 unconstrained permutations that randomized the observations (landscape samples) among classification levels.

First, we investigated the main effects of each predictor variable (E, R, P, and H) independently on the joint response of landscape metrics. Second, we analysed the significance of the two-, three-, and four-way interactions to quantify how E, R, P, and H interact to affect the joint response of landscape metric values. Finally, we conducted separate PERMANOVA analyses for each landscape metric

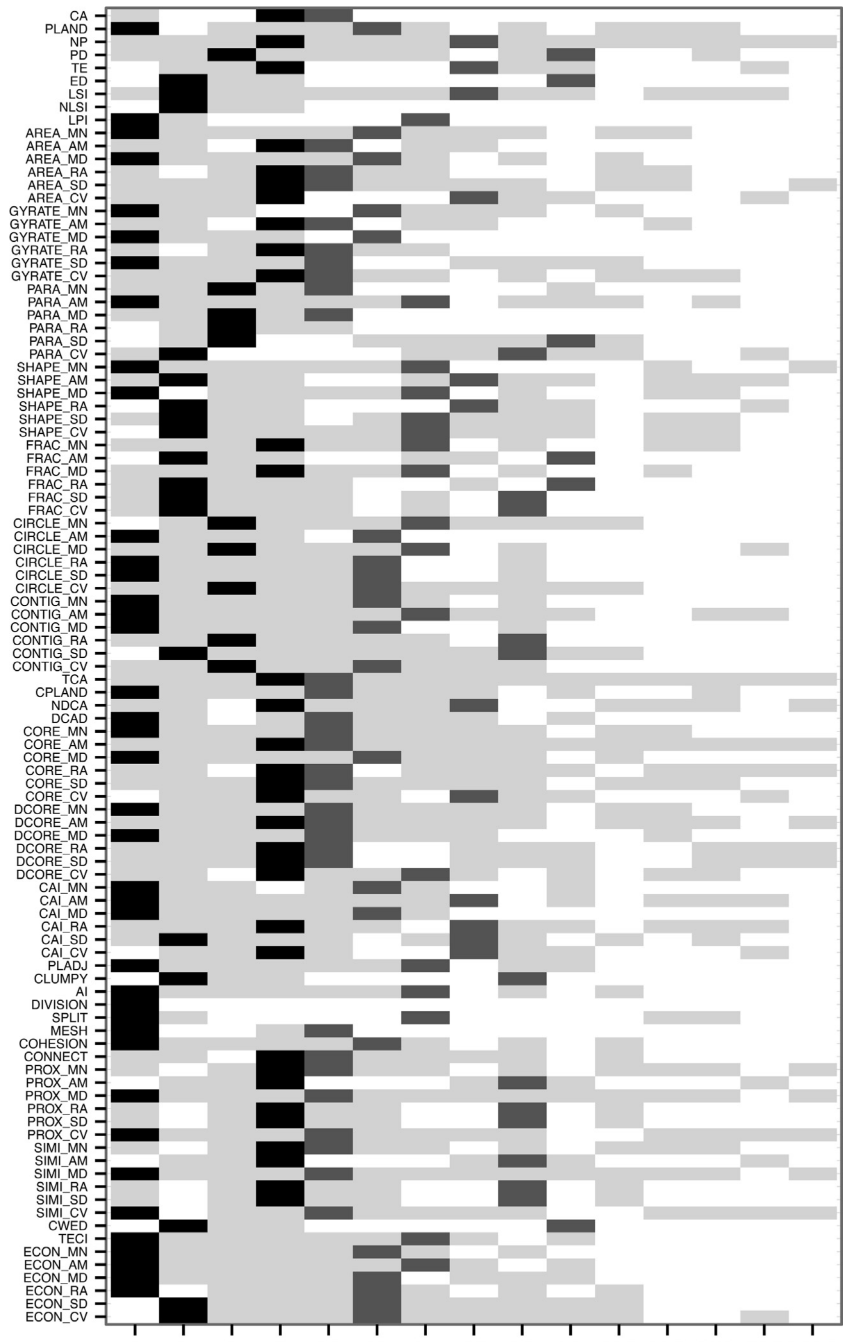

Fig. 1. Summary table of the main effect, two-, three- and four-way interactions of the four predictor variables *P* (percentage of suitable habitat cover), *H* (spatial autocorrelation), *R* (resolution), and *E* (extent). Blank cells indicate no significant interactions (*P*-value ≥ 0.05), light and dark grey and black cells indicate significant interactions. The highest *F*-ratio reported for the combination of explanatory variables per response variable is denoted by the black cells. The second and third highest *F*-ratio are respectively denoted by dark and light grey cells.

separately. We carried out the PERMANOVA using the function `adonis` in the package `vegan` (`R` Development Core Team 2012).

We further assessed interactions between intrinsic and extrinsic characteristics of landscape patterns using interaction plots. The interaction plots describe the mean of the response variable for each level of one predictor variable (e.g. the percentage of suitable habitat cover, *P*) plotted over the levels of a second predictor variable (e.g. the spatial autocorrelation, *H*). The *Y* axis is the dependent variable. Two-way interaction is indicated by non-parallel lines in the resulting plots.

2.3. The self-organizing map clustering technique

To identify less correlated subsets of landscape metrics, we used a self-organizing map (SOM) clustering technique. SOM is a heuristic statistical tool based on methods from machine learning that explores large, complex data sets to detect linear and nonlinear patterns. A detailed description of the SOM methodology can be found in Kohonen (1988). Typically, a SOM is employed as a data reduction and visualization technique that performs a nonlinear projection of multidimensional data onto a map of nodes. The

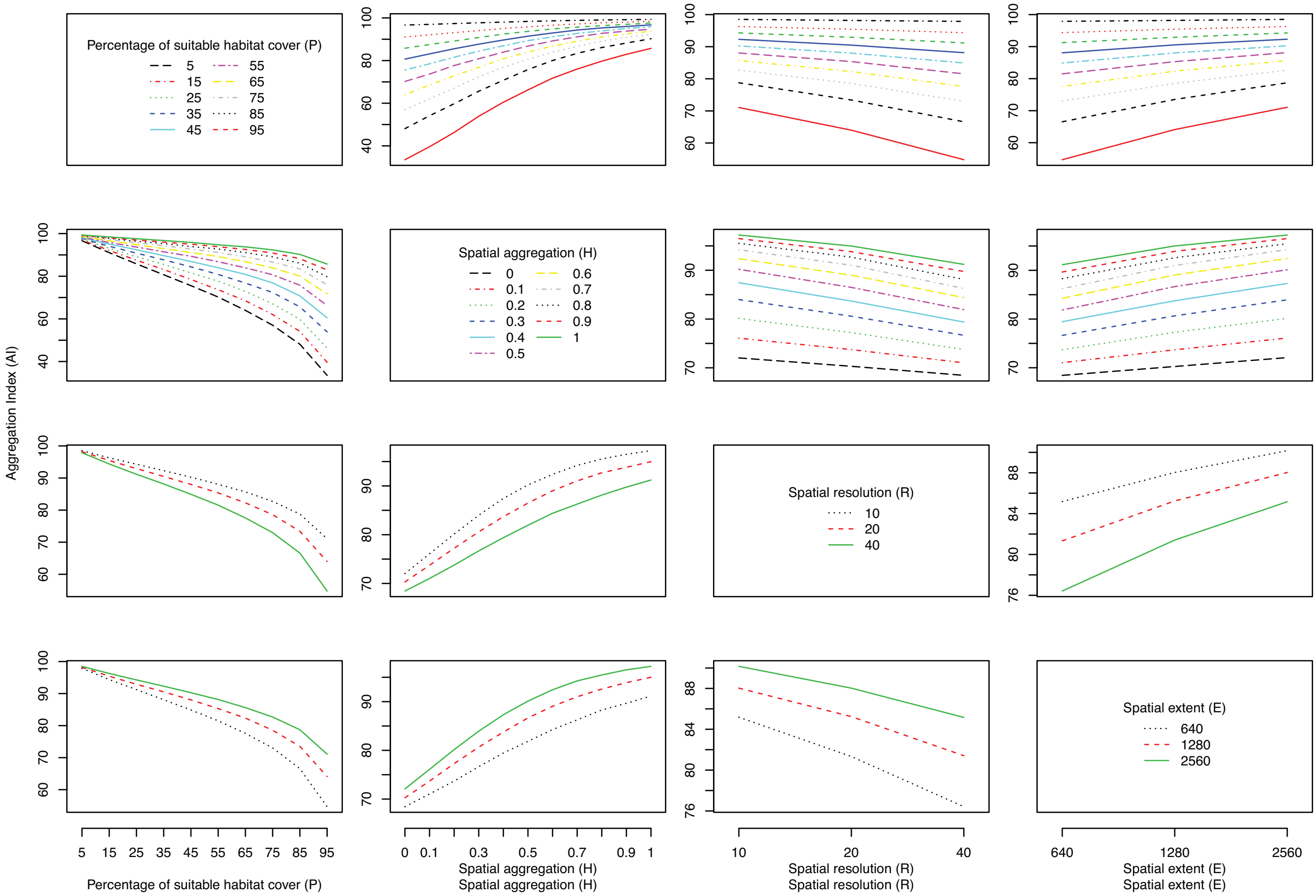

Fig. 2. Two-way interaction plot of the aggregation index (AI) as a representative example of group 1. The profile plots of the group 1 are characterized by non-linear and non-parallel lines indicating possible interactions. However, no complex two-way interactions (bell-shaped curve or cross-over) are observed. The value of the metrics is calculated for all combination of the four predictor variables *P* (percentage of suitable habitat cover), *H* (spatial autocorrelation), *R* (resolution) and *E* (extent).

system learns to represent the input data (landscape metrics) in a way that reflects the statistical structure of the overall collection of the input patterns. Highly correlated landscape metrics are clustered together in specific nodes, whereby nodes that are close together in the map are more alike than nodes that are farther away.

We standardized landscape metrics values. We chose the number of nodes in the output map using the formula $c = 5\sqrt{N}$, where *c* is the number of nodes and *N* is the number of landscape metrics (Vesanto et al., 1999). We then displayed the *U*-matrix (unified distance matrix) to visualize the local Euclidean pair-wise distances

Table 3
Results of the multivariate PERMANOVA based on an Euclidean similarity/dissimilarity of spatial patterns in relation to four predictor variables *P* (percentage of suitable habitat cover), *H* (spatial autocorrelation), *R* (resolution), and *E* (extent) and their interactions. Df = degrees of freedom; SS = sum of squares; MS = mean sum of squares; Pseudo-*F* = *F* value by permutation based on 999 permutations, *P*(perm) = *P*-value (lowest *P*-value possible is 0.001).

	DF	SS	MS	Pseudo-*F*	R^2	*P*(perm)
P	1	18,792	18,791.6	744.80	0.18812	0.001
H	1	10,921	10,921.1	432.86	0.10933	0.001
R	1	11,229	11,228.8	445.05	0.11241	0.001
E	1	15,701	15,700.5	622.29	0.15718	0.001
$P \times H$	1	2177	2176.6	86.27	0.02179	0.001
$P \times R$	1	2763	2763.0	109.51	0.02766	0.001
$H \times R$	1	1183	1183.2	46.90	0.01185	0.001
$P \times E$	1	5940	5940.2	235.44	0.05947	0.001
$H \times E$	1	1953	1953.3	77.42	0.01956	0.001
$R \times E$	1	2210	2210.5	87.61	0.02213	0.001
$P \times H \times R$	1	266	266.2	10.55	0.00266	0.001
$P \times H \times E$	1	578	578.1	22.91	0.00579	0.001
$P \times R \times E$	1	1138	1137.9	45.10	0.01139	0.001
$H \times R \times E$	1	353	353.3	14.00	0.00354	0.001
$P \times H \times R \times E$	1	110	110.2	4.37	0.00110	0.003
Residuals	974	24,574	25.2		0.25	
Total	989	99,889			1.0	

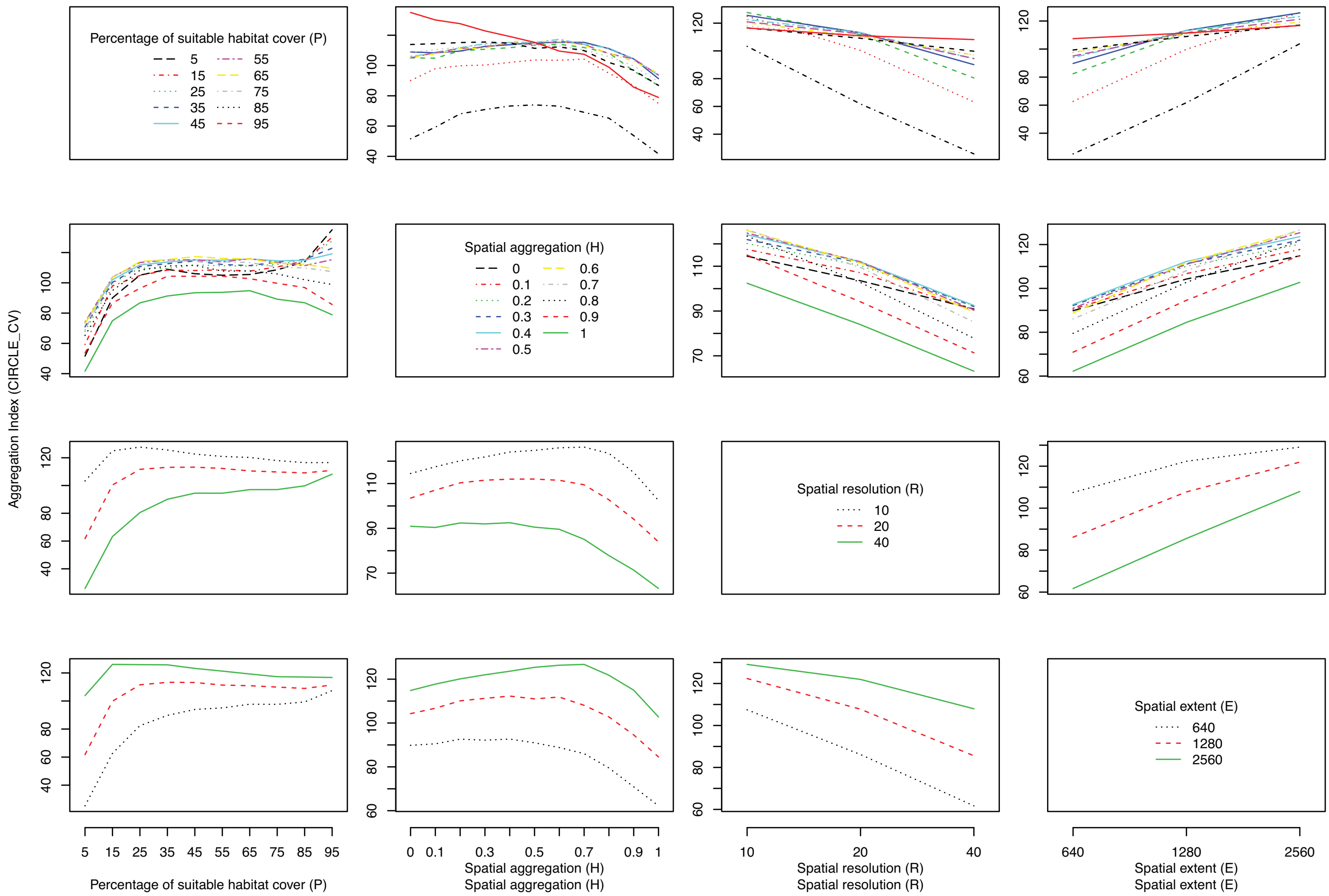

Fig. 3. Two-way interaction plot for the related circumscribing circle metric as a representative example of group 2. The profile plots of the group 2 are characterized by non-linear and non-parallel lines indicating possible significant interactions. No complex two-way interactions are observed when considering changes in *R* and *E* (two bottom lines). However, cross-over and bell-shape curve are observed when considering changes in *P* and *H* (two top lines). The value of the metrics is calculated for all combination of the four predictor variables *P* (percentage of suitable habitat cover), *H* (spatial autocorrelation), *R* (resolution) and *E* (extent).

between neighbouring nodes. To assess the reliability of the results of the SOM methods, we also estimated two commonly used quality measures. We used the quantization error to provide a measure of how good the map reflects the statistical structure of the overall collection of landscape metrics. The quantization error is equalled to the average distance between each of the landscape metrics and its best matching node (Kohonen, 2001). Second, we used the topographic error to measure how well the topology is preserved by the map. It measures the proportion of all landscape metrics for which first and second best matching node are not adjacent units (Kohonen, 2001). We carried out the SOM analysis using the SOM Toolbox for Matlab 5 computing environment (Vesanto et al., 1999).

3. Results

3.1. Multivariate response of landscape metrics

The PERMANOVA provided a novel statistical framework for testing the significance of differences between landscapes. In particular it allowed us to consider the non-linear and complex relations between predictor and response variables. According to the PERMANOVA results, both the extrinsic scale-dependent factors, spatial extent (*E*) and spatial resolution (*R*), and the intrinsic characteristics of landscape patterns, percentage of suitable habitat cover (*P*) and spatial autocorrelation (*H*), significantly contributed to the variation in the similarity/dissimilarity of landscape patterns (Table 3). We observed the same results when testing the independent predictors individually. Overall, the multi-way interactions were significant but showed a smaller contribution to the variation in landscape metric values.

3.2. Univariate response of landscape metrics

The individual responses of landscape metrics to different combinations of the four predictor variables *E*, *R*, *P*, and *H* differed among landscape metrics (Fig. 1). The main effects of the percentage of suitable habitat cover, *P*, or the spatial autocorrelation, *H*, were significant for all landscape metrics indicating that all the selected landscape metrics in this study quantify spatial patterns effectively. In total, only four metrics, the landscape division index (DIVISION), the largest patch index (LPI), the coefficient of variation of the perimeter-area ratio index (PARA_CV) and the splitting index (SPLIT), were not significantly affected by the scale-dependent factors, *H* and *P*.

The metrics fell into three groups. First, eighteen of the 101 metrics were significantly affected by spatial autocorrelation, *H*, but not significantly affected by the proportion of suitable habitat cover, *P*. Examples include the clumpiness index (CLUMPY) or the edge density (ED) that mainly quantify the spatial configuration of landscape patterns as measured by spatial autocorrelation, *H*. However, with the exception of the standard deviation of the perimeter-area ratio index (PARA_SD), all metrics in this group were also significantly affected by a change in both spatial resolution, *R*, and extent, *E*. Second, fifteen of the 101 metrics were significantly affected by the

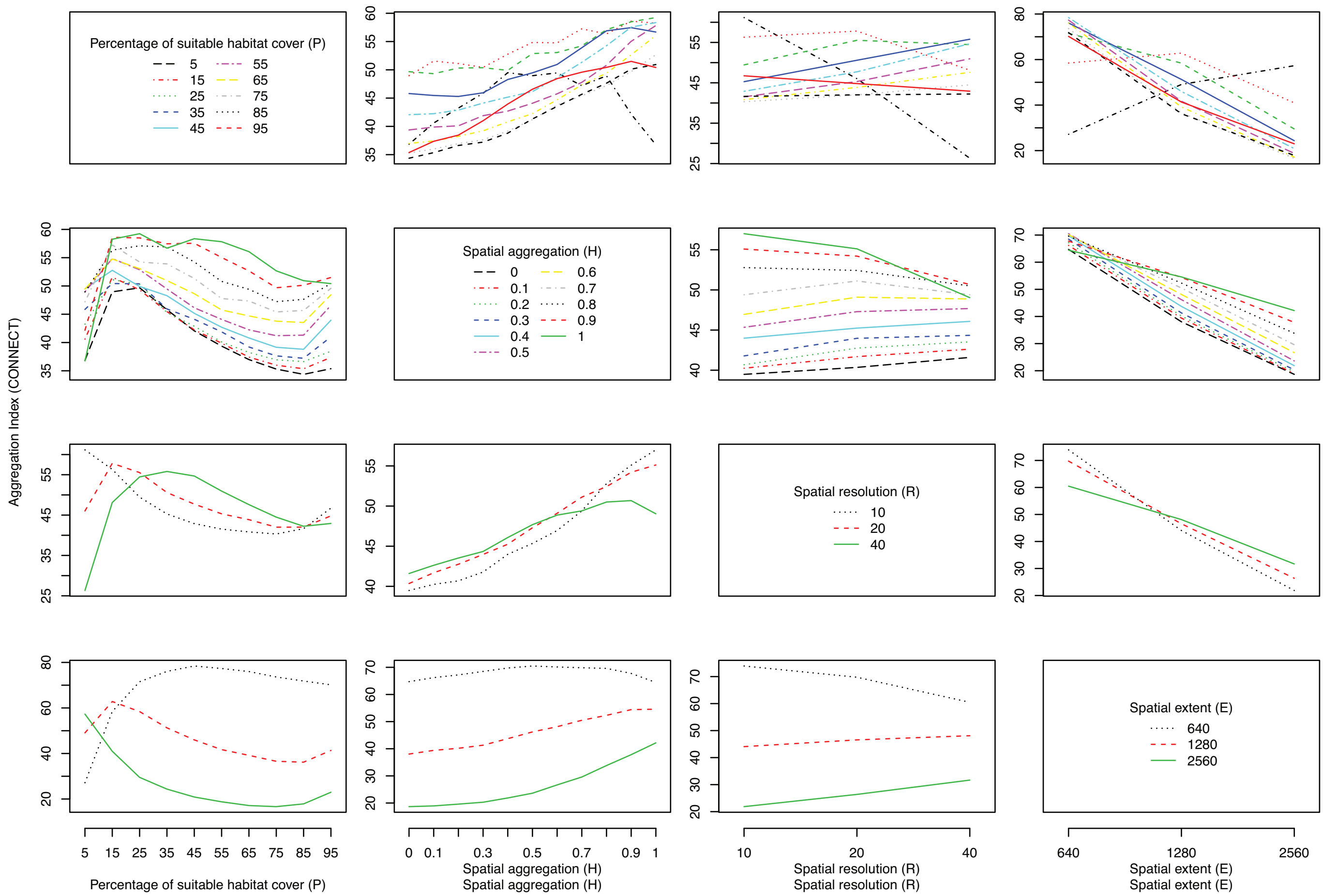

Fig. 4. Two-way interaction plot for the connectance index as a representative example of group 3. The profile plots of the group 3 are characterized by non-parallel and non-monotonic lines indicating complex interactions. Cross-over are observed for most combinations of predictor variables. The value of the metrics is calculated for all combination of the four predictor variables *P* (percentage of suitable habitat cover), *H* (spatial autocorrelation), *R* (resolution) and *E* (extent).

proportion of suitable habitat cover, *P*, but not significantly affected by spatial autocorrelation, *H*. Examples include the effective mesh size (MESH) or the total core area (CA). These metrics mainly quantify the spatial composition of landscape patterns as measured by the percentage of suitable habitat cover, *P*. With the exception of the landscape division index (DIVISION), all metrics in this group were also significantly affected by either a change in extent, *E*, only or by a change in both spatial resolution, *R*, and extent, *E*. Third, sixty-eight of the 101 metrics responded significantly to changing both the proportion of suitable habitat cover, *P*, and spatial autocorrelation, *H*, indicating that the information content of each metric is not a single spatial component, but a complex of several spatial components together. In general, the highest *F*-ratios were reported for a change in extent, *E*, and percentage of suitable habitat cover, *P*. In comparison the change in spatial autocorrelation, *H*, and in spatial resolution, *R*, had a smaller effect on the response variables.

3.3. *Interactions of* E, R, P, *and* H *on the univariate response of landscape metrics*

The results of the PERMANOVA presented a range of two-, three- and four-way interactions. Two metrics, the normalized shape index (nLSI) and the landscape division index (DIVISION), did not respond significantly to factor interactions. Only a few metrics, such as the edge density (ED) or the largest patch index (LPI), responded to a limited number of two-way interactions. Most of the landscape metrics had larger interactions at two or more levels. Generally, the combination of predictor variables $P \times E$, $P \times R$, and, $P \times H$ had greater effect than other combinations of predictor variables. The combination of predictor variables $H \times R$ had on average the smallest two-way interaction effect. The magnitudes of the three-way and four-way interactions were consistently smaller than the two way interactions.

We further analysed the interaction plots for each of the landscape metrics in order to examine the interactions in more detail. Here we found that the metrics fall into three qualitative groups. (1) Metrics, such as the aggregation index (AI), that presented simple monotonic interaction patterns (Fig. 2). As an example, an increase in the percentage of suitable habitat cover, *P*, is always associated with a decrease in AI value. However, this change is more important at smaller extent and higher resolution. The interaction trend remained consistent regardless of the level of the interaction (no cross-over or shape bell were observed). (2) Metrics, such as the coefficient of variation of the related circumscribing circle (CIRCLE_CV), that presented complex interaction patterns (cross-over/bell-shaped) associated with a change in intrinsic characteristics of the landscape, *H* and *P*, only (Fig. 3). While the spatial extent, *E*, and the spatial resolution, *R*, had a significant effect on the value of CIRCLE_CV (Table 3), an increase in spatial extent and spatial resolution was always associated with an increase in CIRCLE_CV without crossed-over in between spatial scale levels. (3) Metrics, such as the connectance index (CONNECT), that showed significant complex two-way interactions associated with both a change in intrinsic characteristics of the landscape, *H* and *P*, and scale-dependent factors, *E* and *R* (Fig. 4).

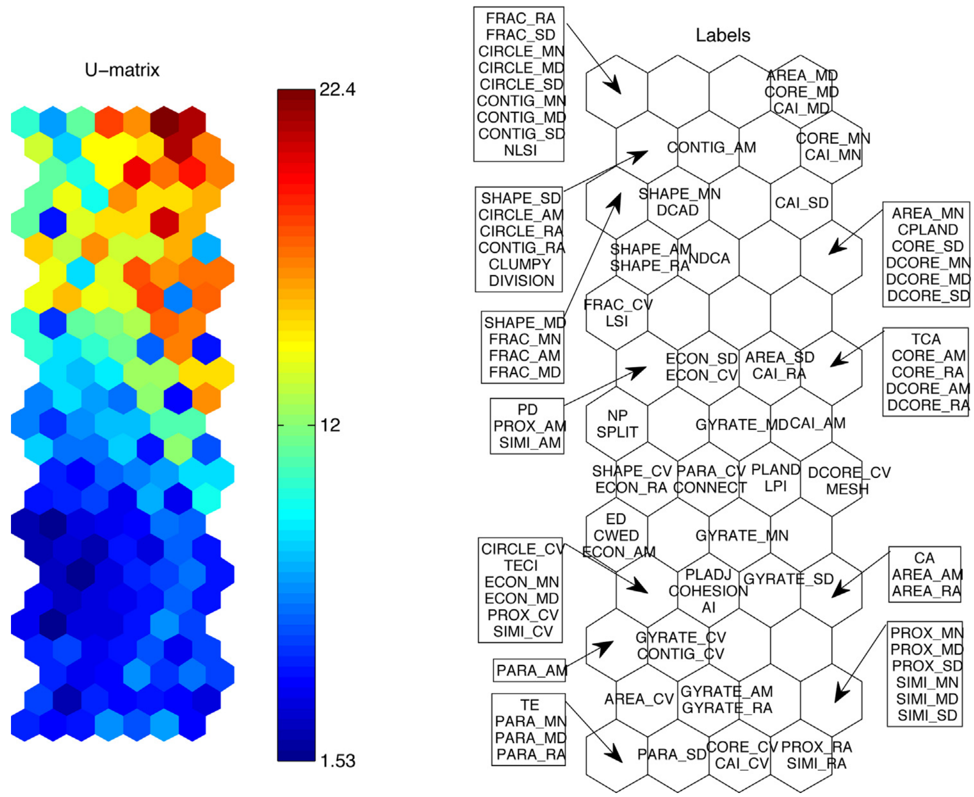

Fig. 5. Clustering of landscape metrics identified with SOM analysis. The panel on the left is a representation of the local Euclidean pair-wise distances between neighbouring SOM nodes depicted in a color scale image. On the right, the name of the landscape metrics are associated with the SOM nodes.

3.4. Extraction of landscape metric patterns

We used the SOM map of 4×13 nodes to organise the metrics into 52 output units identifying metrics with a similar response pattern associated with a change in landscape intrinsic conditions and spatial scales (Fig. 5). The clustering of landscape metrics in the SOM analysis was supported by a negligible topographic error indicating a very good preservation of the initial landscape metric topology.

To visualize the effect of the four predictor variables on the classification of the landscape metrics in the SOM, we calculated, for each output node, the average *F*-ratio of each predictor variables and their two-way interactions (Fig. 6). Dark nodes represent high values while light nodes represent low values. Globally, the average *F*-ratio associated with a change in spatial autocorrelation, *H*, increases from left to right, and the average *F*-ratio associated with a change in both scale-dependent factors, *R* and *P*, increases from the top to the bottom. Looking more closely, the bottom left corner of the map represented metrics strongly affected by spatial resolution, *R*, or the interaction factor $R \times H$ (Fig. 6). The bottom right corner of the map identified metrics strongly affected by a change in spatial extent, *E*, or by the interaction factor $R \times E$. In the upper left, nodes represented metrics most affected by a change in spatial aggregation, *H*, or the interaction factor $H \times P$. Finally, the upper right identified metrics most affected by the interaction factor $P \times E$.

The *U*-matrix reveals that metrics strongly affected by a change in spatial scale (bottom of the map) are closer together, in terms of response to change in predictor variables, than metrics located in the upper part of the map (Fig. 5). The main effect of the spatial extent (*E*), spatial resolution (*R*), percentage of suitable habitat cover (*P*), and spatial aggregation (*H*) and the two-way interaction factors $P \times H$, $H \times R$ and $P \times E$ showed the clearest gradient among predictor variables. This suggests that the two-way interactions are important factors for the classification of landscape metrics, while the effect of the three-way and four-way interaction have less importance.

4. Discussion

4.1. Determining the significance of differences between spatial patterns

This study provides clear evidence that the percentage of suitable habitat cover, *P*, and spatial extent, *E*, accounted for the highest amount of variation of the landscape metrics when compared to spatial autocorrelation, *H*, and spatial resolution, *R*. Variation in these two predictors also tended to result in large main effects and large interactions. On the other hand, each landscape metric appeared to have a unique behaviour in terms of the main effect and interactions of the four predictor variables. As a consequence, results are consistent with previous studies that observed high variability in landscape metric responses to change in spatial conditions (Lechner et al., 2013; Neel et al., 2004) or spatial scale (Wu et al., 2002; Wu, 2004; Šímová and Gdulová, 2012). More broadly, however, the results of our analysis demonstrated that the way in which landscape metrics capture spatial patterns is as much a property of that pattern intrinsic characteristics as it is of scale-dependent factors.

4.2. The importance of interactions in clustering landscape metrics

Our SOM analysis helped identify relationships among metrics that more traditional statistical methods might overlook. It is worth pointing out that the resulting final set of clusters was different than groups of landscape metrics based on conceptual

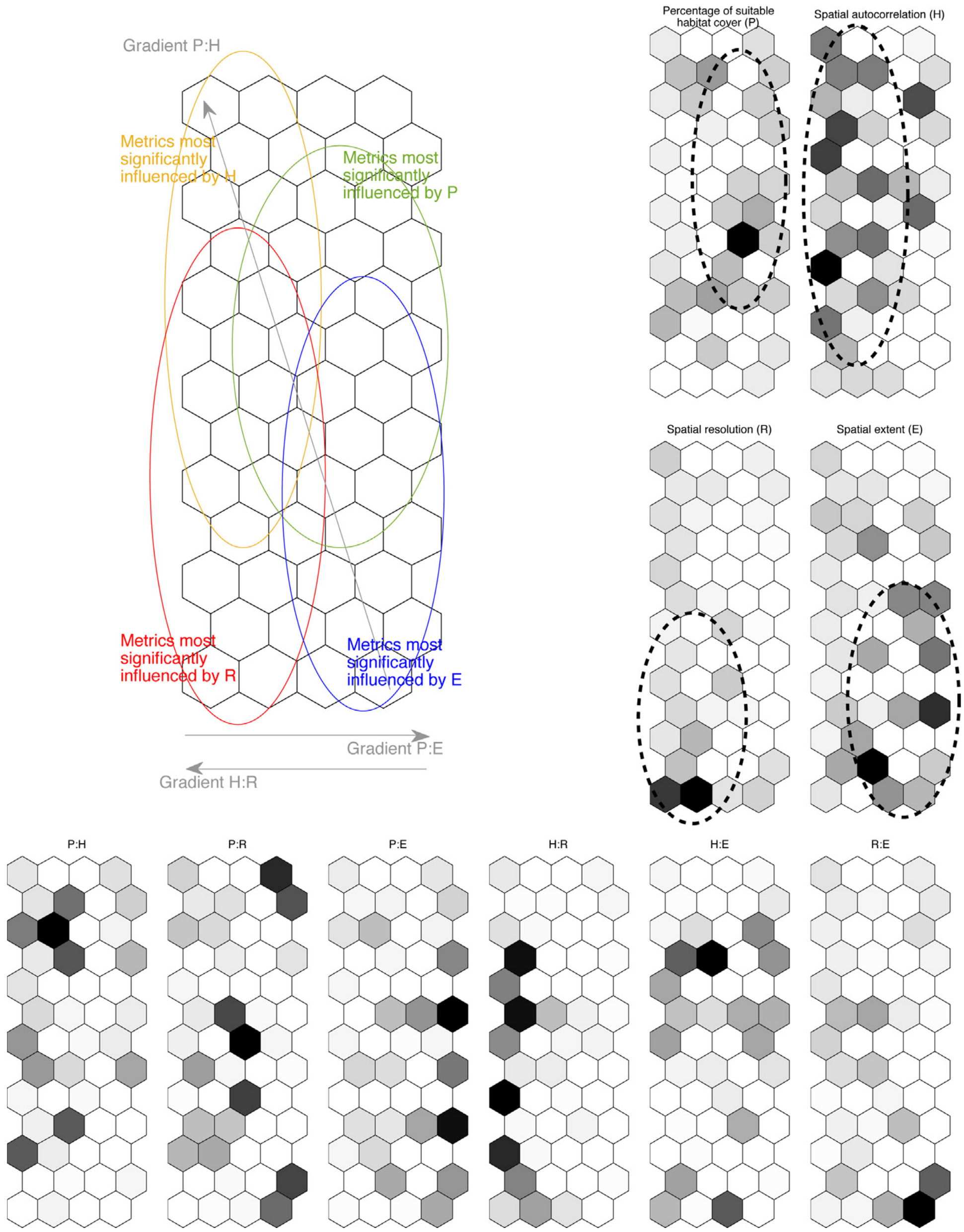

Fig. 6. Visualization of the average *F*-ratio obtained in the PERMANOVA analysis on the SOM map. We calculated the mean *F*-ratio in each nodes of the SOM map for the main effect of the four predictor variables and their two-way interactions. Dark nodes represent high values while light nodes represent low values. The areas with the highest *F*-ratio are marked with a dashed circle. The upper-left graph summarizes the effect of the four predictor variables and their two way interactions in clustering landscape metrics.

similarity (McGarigal et al., 2012) according to the aspect of landscape they supposedly measure. It is common for the practitioner to select metrics from each of these conceptual groups (patch dominance, patch dispersion, nearest neighbour distance, aggregation, patch complexity, edge, contrast, and neighbourhood similarity) to quantify different aspects of the landscape (Cushman et al., 2008; Estreguil et al., 2014). Our results confirmed those of a previous study that emphasize the importance of also considering the behavioural grouping (responses to change in spatial patterns and scale) of landscape metrics (Neel et al., 2004).

More importantly, landscape metrics constitute a highly redundant data-set. To reduce this redundancy, much research focused on a priori selection of independent landscape metrics by evaluating landscape metric response to change of particular components of the landscape (Estreguil et al., 2014; Neel et al., 2004; Turner, 2005). Our results here suggest that landscape metrics present high-order correlations, indicating a need to consider correlations that involve more than just two features. In particular, the two-way interactions between intrinsic characteristics and scale-dependent factors are important factors in patterning landscape metrics.

4.3. Multiple drivers and their interactions

Examination of the interaction plots showed only a small subset of landscape metrics with a monotonic response to interaction factors. For these reduced set of metrics, as long as the final spatial scale is the same, only the magnitude of the difference between the landscapes should change. For example, when comparing two spatial patterns, more heterogeneous spatial patterns will always be characterized as more heterogeneous regardless of the scale of the data. However, most of the metrics presented complex bell-shaped or crossed-over interactions across spatial gradients and spatial scales. This makes extrapolation of responses across spatial scales challenging at best and impossible at worst. The presence of complex interactions indicates that it will be exceedingly difficult to isolate purely landscape pattern driven effects from the effects of changing spatial scale when conducting ecological analyses.

Most previous studies have focused on the main effect of scale-dependent factors and intrinsic characteristics but the interactions among the varied explanatory factors remain poorly understood. The presence of significant complex interactions highlights the importance of considering multiple perspectives for characterizing landscape structure using landscape metrics. For example, one could argue that some landscape metrics exhibit power scaling relationships with change in spatial extent or spatial resolution (Wu, 2004), but this would ignore that numerically speaking, the two-way interactions of scale-dependent factors and intrinsic characteristics are as important as the main effects. Thus, it would be dangerous to conclude from such a biased interpretation about the predictability of landscape metrics behaviour across spatial scale. Such statements are not a criticism of the ability of ecologists to make general predictions about the behaviour of landscape metrics across spatial scales. Rather, our results reaffirm the urgent need to consider the complementary effects of intrinsic and extrinsic characteristics of landscape patterns to conduct integrated landscape pattern assessment (Lechner et al., 2013; Turner, 2005).

5. Conclusion

In this study, we tested the adequacy of 101 landscape metrics to quantify concisely independent aspects of spatial pattern regardless of the scale at which they are represented. The findings highlight the sensitivity of landscape metrics to changes in the intrinsic characteristics (spatial autocorrelation, H, and percentage of suitable habitat cover, P), and scale-dependent factors (spatial extent, E, and spatial resolution, R), individually but also to their interactions. Landscape metric classification essentially resulted from the main effect of the predictor variables and their two-way interactions. The presence of significant complex interactions between intrinsic and extrinsic characteristics of landscape patterns makes it difficult to isolate purely landscape pattern driven effects from the effects of changing spatial scale. As such, our study illustrates the need for more systematic investigation of the relationship between intrinsic characteristics and extrinsic properties when accurate characterization of landscape pattern is a key input in spatially explicit ecological models.

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