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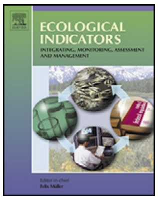

Multiscale performance of landscape metrics as indicators of species richness of plants, insects and vertebrates

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ABSTRACT

Landscape metrics are widely used to investigate the spatial structure of landscapes. Numerous metrics are currently available, yet only little empirical research has comparatively examined their indicator value for species richness for several taxa at several scales. Taking a Mediterranean forest landscape – Dadia National Park (Greece) – as a case study area, we explored the performance of 52 landscape level landscape metrics as indicators of species richness for six taxa (woody plants, orchids, orthopterans, amphibians, reptiles, and small terrestrial birds) and for overall species richness. We computed the landscape metrics for circular areas of five different extents around each of 30 sampling plots. We applied linear mixed models to evaluate significant relations between metrics and species richness and to assess the effects of the extent of the considered landscape on the performance of the metrics. Our results showed that landscape metrics were good indicators for overall species richness, woody plants, orthopterans and reptiles. Metrics quantifying patch shape, proximity, texture and landscape diversity resulted often in well-fitted models, while those describing patch area, similarity and edge contrast rarely contributed to significant models. Spatial scale affected the performance of the metrics, since woody plants, orthopterans and small terrestrial birds were usually better predicted at smaller extents of surrounding landscape, and reptiles frequently at larger ones. The revealed pattern of relations and performances will be useful to understand landscape structure as a driver and indicator of biodiversity, and to improve forest and landscape management decisions in Mediterranean and other forest mosaics.

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1. Introduction

Landscape structure has an important influence on a wide range of ecological patterns and processes, and landscape metrics are common tools to assess these relations under the matrix-corridor-patch model (Forman, 1995; Turner et al., 2001). Development of landscape metrics is ongoing (e.g. McGarigal and Marks, 1995; McGarigal et al., 2009), and their use has increased over the last decade as remote sensing and GIS became standard data sources within biogeography and biodiversity research (Foody, 2008; Gillespie et al., 2008). Landscape datasets are obtainable over large areas (Groom et al., 2006). They enable an extrapolation based on a limited set of ground truth data and provide natural resources managers around the world with real-time data to support conservation efforts (Gaston, 2000; Gillespie et al., 2008). Landscape metrics are applied in systematic reserve design, evaluation of land use change, species habitat requirements, restoration ecology and landscape planning, as sustainability indicators, and as indicators of species richness and biodiversity (Renetzeder et al., 2010; Uuemaa et al., 2009; Walz, 2011). Biodiversity indicators are essential for ecological research, environmental non-governmental organizations, and agencies for nature conservation, forestry and agriculture at local, national and international level (Walz, 2011). Yet a consensus regarding their use has not been reached, and several crucial terms such as landscape heterogeneity and fragmentation are not well defined (Duelli and Obrist, 2003; Fahrig, 2003; Tews et al., 2004). Landscape metrics are potentially very useful indicators of biodiversity (Lindenmayer et al., 2002; Walz, 2011), but results of studies relating landscape structure to species diversity often differ widely. We are far from having a complete picture about the

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indicator value of the metrics for species richness, and depending on the applied landscape metrics and the landscape under consideration, patch size and patch shape can be related to species diversity positively, negatively or not at all (Fahrig, 2003; Torras et al., 2008; Walz, 2011; Yamaura et al., 2008).

A critical factor within landscape analysis is the examined scale (Gustafson, 1998; Walz, 2011; Wu, 2004), characterized by grain size, thematic resolution and extent (Lam and Quattrochi, 1992; Turner et al., 2001). While the response of landscape metrics to grain and thematic resolution behaves rather consistently (Bailey et al., 2007; Wu, 2004; Wu et al., 2002), their response to changing extent (i.e. the map size) does not (Saura and Martinez-Millan, 2001; Wu, 2004). Given a patchy landscape with underlying gradients, at small extents unpredictable behavior of metrics can be caused by too little a sample of patches, while at large extents environmentally different patches might be included in the sample. To discern the important elements of patch structure for a particular organism, an organism-centered view of the landscape must be adopted (Cushman et al., 2008; Li and Wu, 2004; Lindenmayer et al., 2002; Vos et al., 2001). At larger extents landscape structure can influence metapopulation dynamics, and thus, local species richness (Gustafson, 1998; Hunter, 2002; Vos et al., 2001). According to the concept of ecological neighborhood (Addicott et al., 1987), the effects of extent on the performance of landscape metrics as indicators of species richness should depend on the body size, dispersal abilities and life history traits of the taxa under consideration. It can be expected that taxa with larger space demand and of higher mobility are affected by a wider extent of landscape than those that are small and sedentary. This would be in line with the decision hierarchy concept of Holling (1992), which states that spatial grain of habitat perception is a function of body size.

However, the organism-centered view (together with conventional forestry) is unlikely to be successful in maintaining the diversity of forest ecosystems, since landscape approaches and a suite of methods and tools are required for holistic management (Mitchell et al., 2008; Walz, 2011). Regarding landscape metrics and their use as indicators of species richness, it is difficult to define an optimal set of metrics in advance, not least because very few empirical studies have so far explored their indicator value in a comprehensive way and for several taxa at several scales at once (Uuemaa et al., 2009; Walz, 2011). To aid both ecological management and conservation efforts two sets of analyses should be conducted, one describing the major components of landscape structure, and one relating pattern and processes (Cushman et al., 2008; Mitchell et al., 2006). Having recently examined the major components of landscape structure in the Mediterranean forest mosaic of Dadia National Park in Greece (Schindler et al., 2008), in this study we analyzed the performance of landscape level metrics as species richness indicators for the same study area. We screened 52 metrics, each for five different extents of landscape, in order to: (a) provide an overview of their performance for six taxa, i.e. woody plants, orchids, orthopterans, amphibians, reptiles and small terrestrial birds, and for overall species richness, and (b) assess the effect of the extent of the landscape plots on these relations, e.g. if taxa with different space demand and mobility are affected by a different extent of landscape.

2. Methods

2.1. Study area, focal species and land cover data set

Our case study area, the Dadia–Lefkimi–Soufli National Park (centered at 26°10′N, 40°87′E; hereafter Dadia NP) covers 430 km^2 and is located in north-eastern Greece (Fig. 1). The area is dominated by extensive pine (*Pinus brutia*, *P. nigra*) and oak (*Quercus frainetto*, *Q. cerris*, *Q. pubescens*) forest, but it also contains a variety of other habitats such as pastures, arable land, torrents and stony hills. Dadia NP is a well known local biodiversity hotspot (Kati et al., 2004a; Poirazidis et al., 2010, 2011a) and contains the only remaining Black Vulture (*Aegypius monachus*) breeding colony of the Balkan Peninsula (Poirazidis et al., 2004; Skartsi et al., 2008).

We used a data set of six taxonomic groups (189 species), sampled within 30 plots of 20 ha or less, which represented the main vegetation types of the study area (Kati et al., 2004a). The species data set consisted of 48 woody plants, 19 orchids including one rare species (Kati et al., 2000), 38 orthopterans including one endemic species (Kati et al., 2004b), 18 amphibians and reptiles including 5 protected species that are listed under Annex II of Dir 92/43 EE (Kati et al., 2007), and 66 small terrestrial birds, including 23 species of European conservation concern (SPEC 2 & 3) (Kati and Sekercioglu, 2006).

IKONOS satellite images (July 2001, pixel size 1 m in the panchromatic channel and 4 m in the multispectrum) were used for the classification of vegetation types. As more than 55% of the forest belonged to mixed vegetation types (Poirazidis et al., 2010), a quality classification ("Heads up Digitizing") was performed to define individual vegetation patches. We grouped the forest types into "pines", "oaks", and "broadleaves" (broadleaved species other than oaks) and developed categories according to the order of dominance (e.g. "Pines/Oaks", "Pines/Oaks/Broadleaves", "Pines/Broadleaves/Oaks"). Thus, a vector map of 25 habitat categories was obtained (including both forest and non-forest categories), and was further improved using a previously performed supervised classification of vegetation types. For landscape analyses, this habitat map was merged into nine land cover categories (oak forest, pine forest, pine-oak forest, oak-pine forest, broadleaves, openings, fields, roads, and urban areas), and transferred to a raster map with a grain of 5 m (Schindler et al., 2008). For this study, we clipped circular areas of 20, 50, 100, 200 and 500 ha around the centroid of each sampling plot (Fig. 1) and computed for each of these extents landscape metrics at landscape level (McGarigal and Marks, 1995). Following Cushman et al. (2008) and Schindler et al. (2008), we selected 52 metrics in total and kept mean, area-weighted mean and coefficient of variation of the 'Distribution Statistics' (Table 1). To compute the similarity indices and the contrast metrics, we produced a similarity matrix and an edge contrast matrix by assigning similarity and contrast values for each pairwise combination of the nine land cover classes. These values were based on the authors experience in the study area (Schindler et al., 2008).

2.2. Univariate linear mixed models

We tested the indicator value of each individual landscape metric ($n = 52$) at each considered extent ($n = 5$) by using it as a predictor to model the species richness of each taxon, resulting in a total of 260 models per taxon. For this purpose, we assigned the sampling plots to five categorical habitat types – forest (12 plots), shrubs (4), heather (2), grassland (3) and agricultural fields (6). We excluded three plots representing mixed habitats of mosaic character, and created linear mixed models with the categorical habitat type as the random factor of the models (Crawley, 2007). Thus, we could control for the influence of the different habitat types of the sampling plots, which could have masked the effect of the landscape structure. We calculated a pseudo R^2 of the mixed model with a Spearman correlation to compensate for non-normal distribution within the data, and tested for significance. As the primary goal of our study was an exploratory screening of the pattern of indicator values of the landscape metrics, we refrained from correcting the family-wise Type I error rate (Roback and Askins, 2005). Beside other shortcomings, these corrections generally exacerbate the

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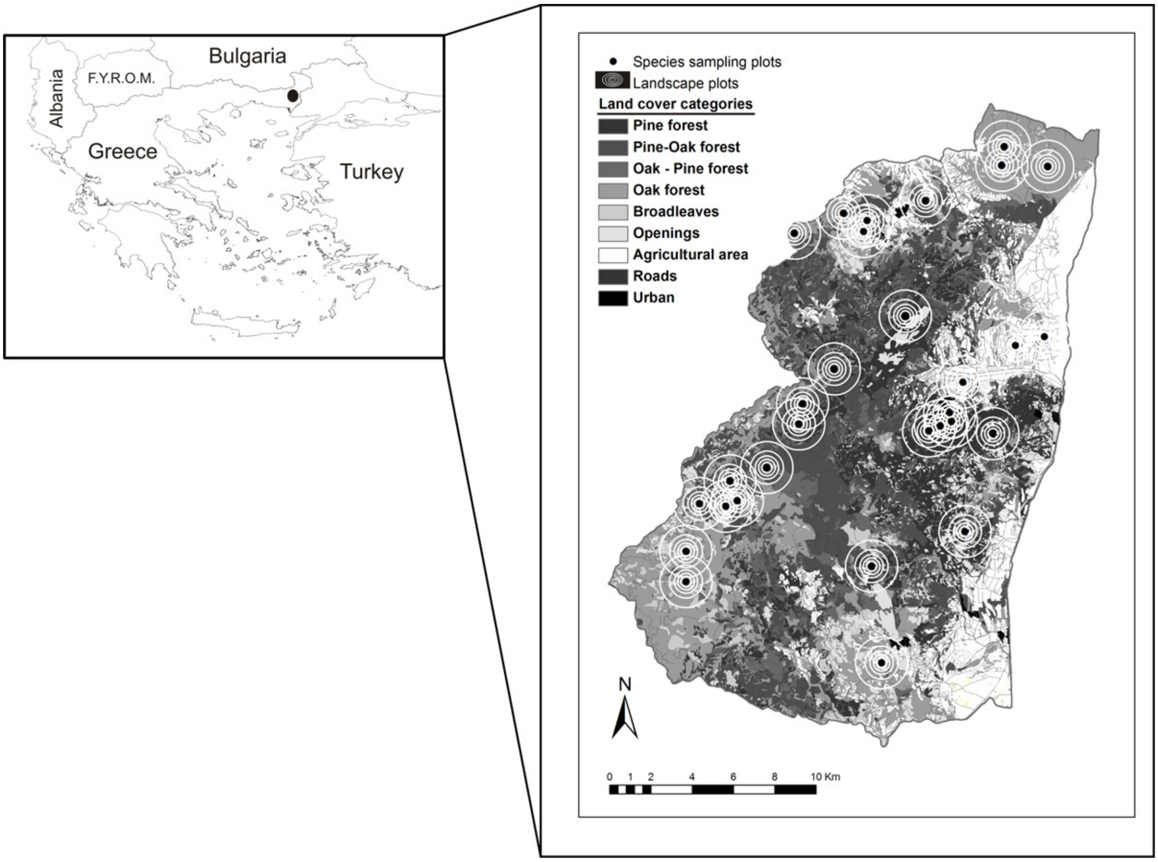

Fig. 1. Dadia National Park, located in NE Greece and raster map of nine land cover categories derived from IKONOS satellite imagery. The circular areas of 20, 50, 100, 200 and 500 ha are shown for each of the 30 sampling plots.

problem of low power in ecological analyses, and lead to the 'hyper-Red Queen paradox' that the more detailed research (i.e., research measuring more variables) researchers do, the less probability they have of finding significant results (Moran, 2003; Nakagawa, 2004).

Such as we did for each taxon, we also computed 260 univariate models for overall species richness. For this purpose, we computed an index of overall species richness (S_{OV}), using the sum of the taxa's relative species richness as a proxy. This way, we could adequately represent species-poor taxa, whereas by simply summing up species richness of all taxa, species-rich taxa receive too big influence on the overall value (Kati et al., 2010). Relative species richness was defined for each taxon as the number of species at a plot $S_{(i,\mathrm{T})}$ divided by the maximum number of species across all 27 sampling plots MAX (S_{T}).

$$S_{\mathrm{OV}} = \sum_{i=1}^{27} \frac{S(i,\mathrm{T})}{\mathrm{MAX}(ST)}$$

In an additional approach, we grouped the landscape structure variables into the six categories area, shape, isolation, contrast, texture and diversity (Schindler et al., 2008), and evaluated for each taxon (and overall species richness) and each extent the number of categories containing at least one significant model (cf. Table 3).

We used R (R Development Core Team, 2008) to perform the statistical analyses and Fragstats 3.2 and ArcGIS 9.1 to derive and process the landscape variables.

3. Results

Landscape metrics resulted in significant models for woody plants, orthopterans, reptiles, small terrestrial birds and overall species richness (Table 2), while virtually no significant relations were detected between the metrics and species richness of orchids (only in two out of 260 models) or amphibians (only in four out of 260 models).

Landscape metrics quantifying patch shape, proximity, texture, diversity and patch size were often significant predictors within univariate models, while metrics regarding similarity or contrast of neighboring patches hardly yielded any significant model (Table 2). Regarding the metrics based on distribution statistics (cf. Table 1), the area-weighted mean (AM) regularly outperformed both the mean (MN) and the coefficient of variation (CV) of the variables. The Coefficient of Variation of the Patch Fractal Dimension (FRAC_CV) for a surrounding area of 500 ha was the best performing indicator, strongly related to low species richness of orthopterans, amphibians, small terrestrial birds (all $p < 0.05$), woody plants ($p < 0.01$) and overall species richness ($p < 0.01$). Some metrics obtained significant relations to the species richness of one particular taxon at several extents, but at no extent to any other taxon. Examples of such taxon specific metrics were ED, LSI, CONTIG_AM, PLADJ and AI for woody plants and PAFRAC and GYRATE_CV for orthopterans (compare Table 1 for the explanation of the abbreviations and McGarigal and Marks, 1995 for further information). Several metrics showed significant relations to overall species richness; but not any to any single taxon (Table 2). The metrics PARA_MN; CONTIG_MN; CONTIG_CV; SIMI_AM; TECI; ECON_MN; and ECON_CV did not result in any significant univariate model for any combination of taxon and extent.

Spatial extent affected the number of landscape metrics that obtained significant relations to species richness. Although single metrics generally performed better at small and intermediate extents (Table 2), some important exceptions were detected, such

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Table 1
52 landscape level landscape metrics tested in this study. Regarding the distribution statistics (DSt), we used mean (MN), area weighted mean (AM) and coefficient of variation (CV). For complete descriptions, see McGarigal and Marks (1995).

Acronym	Metric name	Number	Description
Category I. Patch size & patch density		*8*	
AREA	Patch Area	3	DSt; size of the patches
GYRATE	Radius of Gyration	3	DSt; radius of gyration, i.e. the mean distance for each cell of one patch to the patch centroid
PD	Patch Density	1	Number of patches per area
LPI	Largest Patch Index	1	Percentage of total area occupied by the largest patch
Category II. Edge & patch shape		*15*	
LSI	Landscape Shape Index	1	Ratio of the total edge to the minimum total edge
ED	Edge Density	1	Total length of edge per unit area
SHAPE	Shape Index	3	DSt; equals 1 when all patches are circular; increases with complexity of patch shapes; independent of patch size
PARA	Perimeter-Area Ratio	3	DSt; patch shape complexity measure that measures perimeter per area
FRAC	Fractal Dimension Index	3	DSt; patch shape complexity measure that approaches 1 for simple shapes and 2 for complex shapes
CONTIG	Contiguity Index	3	DSt; equals 0 for a one-pixel patch and approaches 1 as patch contiguity, or connectedness increases
PAFRAC	Perimeter-Area Fractal Dimension	1	Patch shape complexity measure, which approaches 1 for shapes with simple perimeters and 2 for complex shapes
Category III. Edge contrast		*5*	
CWED	Contrast-Weighted Edge Density	1	Total amount of edge per area, weighted by the contrast between the different land cover types
TECI	Total Edge Contrast Index	1	Ratio of the contrast weighted total length of edge to the not-contrast weighted total length of edge per grid
ECON	Edge Contrast Index	3	DSt; ratio of the contrast weighted to the not-contrast weighted edge length per patch
Category IV. Isolation, proximity & similarity		*9*	
PROX	Proximity Index	3	DSt; considers size and proximity of all patches with the same land cover type inside a specified search radius
SIMI	Similarity Index	3	DSt; considers size and proximity of patches within a search radius, weighted by their similarity to the focal patch
ENN	Euclidean Nearest Neighbor Distance	3	DSt; minimum edge to edge distance to the nearest neighboring patch of the same type
Category V. Texture		*6*	
CONTAG	Contagion Index	1	Measure of the aggregation of the land cover classes
PLADJ	Percentage of Like Adjacencies	1	Percentage of neighboring pixel, being the same land cover class, based on double-count method
AI	Aggregation Index	1	Percentage of neighboring pixel, being the same land cover class, based on single-count method
IJI	Interspersion & Juxtaposition Ind. (%)	1	Measure of evenness of patch adjacencies, equals 100 for even and approaches 0 for uneven adjacencies
DIVISION	Landscape Division Ind. (Proportion)	1	Equals the probability that 2 randomly chosen pixels in the landscape are not situated in the same patch
SPLIT	Splitting Index	1	Equals the number of patches of a landscape divided into equal sizes keeping landscape division constant
Category VI. Diversity		*9*	
PR	Patch Richness	1	Equals the number of patch types
PRD	Patch Richness Density (no./100 ha)	1	Equals the number of patch types (i.e. land cover categories) per 100 ha
RPR	Relative Patch Richness	1	Percentage of present patch types out of all categories
SIDI	Simpson's Diversity Index	1	Diversity measure, which equals 1 minus the sum of the squared proportional abundance of each patch type
SHDI	Shannon's Diversity Index	1	Equals minus the sum of the proportional abundance of each patch type multiplied by the ln of that proportion
MSIDI	Modified Simpson's Diversity Index	1	Diversity measure, which equals minus the ln of the sum of the squared proportional abundance of each patch type
SHEI	Shannon's Evenness Index	1	Diversity measure, which considers only evenness of patch sizes, not the number of patches
SIEI	Simpson's Evenness Index	1	Diversity measure, which considers only evenness of patch sizes, not the number of patches
MSIEI	Modified Simpson's Evenness Index	1	Diversity measure, which considers only evenness of patch sizes, not the number of patches
SUM		52	

as FRAC_CV and the Coefficient of Variation of the Radius of Gyration (GYRATE_CV). Orthopterans and small terrestrial birds were better indicated by landscape metrics at smaller extents of 20–50 ha, woody plants and overall species richness at extents of 20–200 ha, while models for reptiles performed best at extents of 200 and 500 ha (Table 2). A similar pattern was revealed regarding the number of categories of metrics (i.e. patch size category, patch shape category, diversity category, etc.) containing at least one significant model. While the number was stable throughout all extents for reptiles and overall species richness, it declined from smaller to larger extents for woody plants, orthopterans, and small terrestrial birds (Table 3).

4. Discussion

4.1. Landscape metrics as indicators of species richness

Our analyses revealed that the indicator value of landscape metrics strongly depends on the taxon examined. We detected a strong indicator value of landscape metrics for overall species richness, woody plants, orthopterans and reptiles, while the performance of the metrics was poorer for small terrestrial birds and the poorest for orchids and amphibians. The results for woody plants confirm that a high species richness of can be indicated by a surrounding landscape of fine texture and high edge density. This could have been expected according to the habitat heterogeneity hypothesis (e.g. McArthur and Wilson, 1967) and the intermediate disturbance hypothesis (Connell, 1978). Total phytodiversity may show an even stronger peak at disturbed habitats, but woody plants are also adapted to disturbance. Tree diversity in Spain (Torras et al., 2008) and plant diversity in Western Europe (Dufour et al., 2006; Honnay et al., 2003) are strongly related to landscape diversity, while the effects of patch shape are not consistent. These outcomes contrast results from tropical forests, although tropical plant diversity should also peak at intermediate disturbances (Connell, 1978; Kessler, 2001). Hill and Curran (2003) studied tree diversity in Ghana, which mostly depends on the total area of the forest fragments and to a lesser amount on other aspects of landscape structure. In Mexican forests, the diversity of trees, shrubs and vines is hardly affected by patch area, but strongly affected by patch shape and negatively affected by landscape diversity (Hernández-Stefanoni, 2006). Orchid species richness, on the other hand, was

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Table 2
Pattern of performance of landscape metrics as indicators of species richness at different spatial extents (20–500 ha). "+", "—" indicate direction of relation. Letters indicate $p < 0.05$, W = woody plants, X = orchids, O = orthopterans, R = reptiles, A = amphibians, B = small terrestrial birds, ** indicates $p < 0.01$, subscripts are the values of Spearman's ρ. For the models for overall species richness, bright grey background shows significance $p < 0.05$ ($0.38 < \text{Spearman's } \rho < 0.57$), dark grey background $p < 0.01$ ($0.49 < \rho < 0.6$). PARA_MN, CONTIG_MN, CONTIG_CV, SIMI_AM, TECI, ECON_MN and ECON_CV did not result in any significant model for any taxa or extent and were not presented in the overview.

Metric	+/—	20 ha	50 ha	100 ha	200 ha	500 ha
Category I. Patch size & patch density						
AREA_MN	—					
AREA_AM	—					
AREA_CV	+	$\mathbf{W}_{0.42}$ $\mathbf{O}_{0.53}$ $\mathbf{B}_{0.51}$				
GYRATE_MN	—	$\mathbf{O}_{0.43}$ $\mathbf{R}_{0.72}$				
GYRATE_AM	—			$\mathbf{W}_{0.40}$		
GYRATE_CV	—				$\mathbf{O}_{0.41}$	$\mathbf{O}_{0.43}$
PD	+	$\mathbf{W}_{0.44}$ $\mathbf{B}_{0.48}$	$\mathbf{O}_{0.49}$	$\mathbf{W}_{0.39}$		
LPI	—					
Category II. Edge & patch shape						
LSI	+	$\mathbf{W}_{0.43}$	$\mathbf{W}^{**}_{0.50}$	$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.41}$	
ED	+	$\mathbf{W}_{0.43}$		$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.41}$	
SHAPE_MN	—	$\mathbf{O}_{0.49}$		$\mathbf{R}_{0.71}$		$\mathbf{W}_{0.40}$
SHAPE_AM	+	$\mathbf{W}_{0.43}$ $\mathbf{B}_{0.51}$	$\mathbf{W}_{0.45}$ $\mathbf{B}_{0.56}$	$\mathbf{W}_{0.45}$		
SHAPE_CV	—		$\mathbf{A}_{0.89}$			
PARA_AM	+	$\mathbf{W}_{0.43}$	$\mathbf{W}^{**}_{0.67}$ $\mathbf{O}_{0.48}$	$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.41}$	
PARA_CV	+		$\mathbf{W}_{0.53}$ $\mathbf{R}_{0.74}$ $\mathbf{B}_{0.60}$			
FRAC_MN	—					
FRAC_AM	+	$\mathbf{W}_{0.47}$ $\mathbf{B}_{0.54}$	$\mathbf{W}_{0.43}$ $\mathbf{B}_{0.58}$		$\mathbf{B}_{0.42}$	
FRAC_CV	—	$\mathbf{O}_{0.42}$		$\mathbf{W}_{0.39}$ $\mathbf{O}_{0.46}$	$\mathbf{W}_{0.43}$ $\mathbf{O}^{**}_{0.54}$	$\mathbf{W}^{**}_{0.52}$ $\mathbf{O}_{0.40}$ $\mathbf{B}_{0.55}$
CONTIG_AM	—	$\mathbf{W}_{0.42}$	$\mathbf{W}^{**}_{0.50}$	$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.41}$	
PAFRAC	—	$\mathbf{O}^{**}_{0.58}$			$\mathbf{O}_{0.62}$	$\mathbf{O}^{**}_{0.64}$
Category III. Edge contrast						
CWED	+	$\mathbf{B}_{0.44}$				
ECON_AM	+	$\mathbf{B}_{0.44}$				
Category IV. Isolation, proximity & similarity						
PROX_MN	—	$\mathbf{O}_{0.53}$ $\mathbf{R}_{0.70}$	$\mathbf{O}^{**}_{0.55}$ $\mathbf{R}_{0.68}$	$\mathbf{R}^{**}_{0.80}$	$\mathbf{R}_{0.73}$	
PROX_AM	+/—	$\mathbf{R}—_{0.74}$	$\mathbf{A}+^{**}_{0.91}$			$\mathbf{R}—_{0.73}$
PROX_CV	+	$\mathbf{O}^{**}_{0.60}$				
SIMI_MN	—					
SIMI_CV	—	$\mathbf{X}_{0.71}$				
ENN_MN	+					
ENN_AM	+	$\mathbf{W}_{0.39}$ $\mathbf{B}_{0.55}$	$\mathbf{O}_{0.49}$			
ENN_CV	+/—	$\mathbf{B}+_{0.54}$	$\mathbf{X}—^{**}_{0.75}$			$\mathbf{A}+_{0.90}$
Category V. Texture						
CONTAG	—		$\mathbf{O}_{0.47}$ $\mathbf{R}_{0.68}$		$\mathbf{R}_{0.71}$	$\mathbf{R}_{0.70}$
PLADJ	—	$\mathbf{W}_{0.43}$	$\mathbf{W}^{**}_{0.50}$	$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.41}$	
AI	—	$\mathbf{W}_{0.43}$	$\mathbf{W}^{**}_{0.50}$	$\mathbf{W}_{0.47}$	$\mathbf{W}_{0.40}$	
IJI	+		$\mathbf{O}_{0.48}$			
DIVISION	+					
SPLIT	+		$\mathbf{W}_{0.43}$	$\mathbf{W}^{**}_{0.55}$	$\mathbf{W}^{**}_{0.51}$	
Category VI. Diversity						
PR	+	$\mathbf{O}_{0.48}$				
PRD	+	$\mathbf{O}_{0.48}$				
RPR	+	$\mathbf{O}_{0.48}$				
SHDI	+	$\mathbf{O}_{0.44}$ $\mathbf{R}_{0.69}$	$\mathbf{O}_{0.49}$		$\mathbf{R}_{0.71}$	$\mathbf{R}_{0.72}$
SIDI	+	$\mathbf{O}_{0.39}$	$\mathbf{O}_{0.44}$ $\mathbf{R}_{0.69}$	$\mathbf{R}_{0.69}$	$\mathbf{R}_{0.71}$	$\mathbf{R}_{0.72}$
MSIDI	+	$\mathbf{O}_{0.40}$	$\mathbf{O}_{0.46}$			$\mathbf{R}_{0.72}$
SHEI	+		$\mathbf{O}_{0.49}$		$\mathbf{R}_{0.70}$	
SIEI	+		$\mathbf{O}_{0.46}$ $\mathbf{R}_{0.69}$	$\mathbf{R}_{0.69}$	$\mathbf{R}_{0.71}$	$\mathbf{R}_{0.71}$
MSIEI	+		$\mathbf{O}_{0.47}$			$\mathbf{R}_{0.70}$

not indicated by the surrounding landscape structure. Orchids are stenoecious organisms and their species richness seems to be mainly affected by their need for oligotrophe and sunny microhabitats of medium disturbance (Kati et al., 2000, 2010; Mitchley and Xofis, 2005). Landscape analyses are seemingly too coarse in extent and thematic resolution to produce well-performing indicators for orchids.

Orthopteran richness peaks in Dadia NP in open oak forest with thermophilous scrub undergrowth and wet grassy undergrowth (Kati et al., 2004b). At small landscape extents, our results show that orthopteran species richness was best indicated by high landscape diversity, while at large extents, patch shape metrics (FRAC_CV and PAFRAC, but not the other metrics) had partly a good performance. Batáry et al. (2007) detected little effect of landscape structure on orthopterans in Hungarian grasslands, but found that the most abundant species are even more abundant in homogenous landscapes. Amphibians are also stenoecious due to their dependence on water microhabitat diversity (Kati et al., 2007). This factor was not well covered by our study, mainly since small streams are covered by canopy and invisible on the satellite images. A further problem might be that amphibians were the taxon with lowest maximum species richness, thus the gradient of species richness

Table 3
Relations between landscape structure, organism groups and scale (i.e. extent of the landscape plot) expressed by the number of categories of univariate models (out of the six categories "area", "shape", "contrast", "isolation", "texture", and "diversity") containing at least one model with significant indication of species richness.

Taxon	Extent in ha				
	20	50	100	200	500
Woody plants	4	2	3	2	1
Orchids	1	1	0	0	0
Orthopterans	4	5	1	2	2
Amphibians	0	2	0	0	1
Reptiles	3	4	3	3	3
Small terrestrial birds	4	1	0	1	1
Overall species richness	5	6	5	5	5

was shorter and it was more difficult to obtain significant results. For these reasons, the detected pattern that landscape metrics were bad performing indicators of amphibian species richness must be considered cautiously. Atauri and De Lucio (2001) showed for central Spain that diversity of both amphibians and reptiles increases with increasing landscape heterogeneity, patch density and naturalness. Regarding reptiles, we found that landscape diversity at a micro- and meso-scale is a good performing indicator of high species richness, as do other ecological factors such as the type of substrate or the degree of shade in the study area (Kati et al., 2007). On the other hand, landscape metrics regarding other aspects of landscape structure rarely were valid predictors of reptile species richness. Only the Mean Proximity Index and Contagion enabled valid models, but these metrics, being measures of aggregation and land cover dominance, are strongly correlated with the diversity indices (Schindler et al., 2008; Turner, 2005). Landscape heterogeneity and patch density do enhance avian diversity in case studies from Spain (Atauri and De Lucio, 2001; Pino et al., 2000) and the south-eastern USA (Mitchell et al., 2006, 2008). Avian species richness in Dadia NP is related to landscape heterogeneity (Kati and Sekercioglu, 2006; Kati et al., 2010), but it was poorly indicated by our set of landscape level metrics. Only convoluted shapes in close vicinity of the sampling plots were of predictive value for an increased level of species richness. Reasons for the poor performance of landscape metrics as indicators for avian species richness may include the high mobility of birds. Therefore, homogeneity, isolation or poor connectivity of surrounding landscape might have less of an effect on the metapopulation dynamics and species richness of birds than on ground dwelling taxa. Furthermore, several guilds of birds are included in the data, which might even out different preferences of landscape structure (Mitchell et al., 2006, 2008; Pino et al., 2000; Yamaura et al., 2008).

In this study, we detected that several landscape metrics indicated overall species richness much better than that of any single taxon. These cases are of special interest, as they imply that the good overall performance was not caused by a very strong relation to a single taxon, but by a general pattern across most of the taxa. For our study area, woody plants and small terrestrial birds are considered the best surrogate taxa of overall species richness (Kati et al., 2004a, 2010). One reason for the good indicator value of these taxa might be, that they were the richest in species, thus for the current study we used an index of overall species richness, which was robust against differences in species richness among the taxa. However, two recent reviews pinpoint contrasting results of surrogate value among groups, dependent on the method, scale and selected taxon (Cabeza et al., 2008; Rodrigues and Brooks, 2007).

4.2. Comparison among metrics

Metrics quantifying both aspects of landscape structure – composition (e.g. diversity) and configuration (e.g. texture and patch shape) – were valuable indicators of species richness (Andrén, 1994; Mitchell et al., 2006; Vos et al., 2001). While particular species might need continuous and large patches, species richness for the studied taxa was always indicated by increased habitat diversity, patch and edge density. These results should be considered in conservation management of heterogeneous Mediterranean forest landscapes (Kati et al., 2004b; Pino et al., 2000; Rocchini et al., 2006) and are similar to results revealed throughout Europe. Wrbka et al. (1999, 2008) proved for plants, birds and bryophytes of Austria that species richness is positively related to landscape diversity, corresponding with results for plants in Belgium (Honnay et al., 2003) and for trees (Torras et al., 2008), butterflies, herpetofauna and birds (Atauri and De Lucio, 2001) in Spain. Regarding the texture metrics, all but IJI were good indicators of overall species richness, Contagion performed particularly well for reptiles, and PLADJ, AI and SPLIT for woody plants. Other metrics, e.g. the ones regarding edge contrast and similarity, generally performed worse. Due to anthropogenic disturbance, a wide range of contrast intensities appeared in most of the landscape samples. Probably the effects of contrast metrics can neutralize each other over whole taxa, while they are important for specialized species such as the Redback Salamander (*Plethodon cinereus*) in North-American hardwoods (De Graaf and Yamasaki, 2002). However for tropical forests, Hernández-Stefanoni (2006) revealed that high edge contrast is related to lower species richness of the three groups of plants he was investigating, i.e. trees, shrubs and vines.

In this study, the metrics of the patch shape group were particularly good indicators of overall species richness and diversity of woody plants. Regarding the distribution statistics of this group, the area-weighted means performed better than the means, providing evidence that area-weighted metrics are ecologically more meaningful as suggested by Gustafson (1998). According to Saura (2002), however, large patches tend to have more irregular shapes, thus landscapes with larger patches could represent higher values for area-weighting patch shape indexes. This may cause them to be more related to patch size than to patch shape (Torras et al., 2008). Previous research revealed that irregular patch shape can indicate both high and low plant diversity (Hernández-Stefanoni, 2006; Torras et al., 2008), and Yamaura et al. (2008) detected for Japanese boreal forests that irregular patch shapes have a positive effect only on edge species, while the effect is negative for interior species.

4.3. Effects of scale (i.e. landscape extent)

The effects of landscape structure on species richness depended strongly on the spatial scale, since no variable was constantly significant across all landscape extents for any taxon. An interesting pattern regarding scale was that an upper limit of relevant spatial extent was detected for all taxa but reptiles. The threshold between 100 and 500 ha does not necessarily imply that the animals cover such large home ranges, but rather that the landscape structure surrounding the sampling plots affects their metapopulation dynamics. Some metrics that performed particularly well at the larger extents are FRAC_CV and GYRATE_CV. One reason might be that for these complex distribution statistics (both quantify the statistical spread of patch shape, in the case of GYRATE combined with patch size) a larger extent is needed for their effects to become noticeable. The good performance of many metrics at the extent of 20 ha implies that this extent contains a representative sample of patches and thus enables fine scale modeling, at least with high resolution earth observation data in a heterogeneous landscape. While the indicator value of the metrics varied strongly with spatial scale, the most important components of landscape structure are rather stable across scales (Cain et al., 1997; Schindler et al., 2008). We recommend widening scale research towards a comprehensive

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investigation of scale effects on the indicator values and other ecological applications of landscape metrics.

4.4. Implications for landscape and forest management

In Dadia National Park, land abandonment and homogenization of landscape have already taken place, and have lead to an important decrease of landscape heterogeneity compared with some decades ago (Poirazidis et al., 2010). As conservation measures for safeguarding local biodiversity, maintenance of forest openings in the buffer zone, maintenance of forest heterogeneity, and enhancement of periodical livestock grazing have been suggested (Kati and Sekercioglu, 2006; Kati et al., 2004b; Schindler et al., 2011). Our results clearly support the above measures, as landscape heterogeneity indicated high species richness of several biological groups. The preservation of a mosaic character appears to be crucial for the conservation of biodiversity in landscapes of several parts of the Mediterranean biodiversity hotspot (Myers et al., 2000) such as Greece, Italy and Spain (Atauri and De Lucio, 2001; Farina, 1997; Pino et al., 2000; Rocchini et al., 2006; Torras et al., 2008). The Mediterranean spatial heterogeneity imitates that of a permanent disturbance regime and is threatened by land abandonment that leads to woodland recovery and a reduction of open space (Farina, 1997).

Sustainable forest management should consider the maintenance of biodiversity and other traditionally undervalued ecosystem functions (Kohm and Franklin, 1997; United Nations, 1992). Management that leads to heterogeneous and convoluted forest patches should be promoted instead of intensive production forest, typically managed as mono-specific stands (Gil-Tena et al., 2007). An increased use of the forested area for the production of non-timber products may also be positive for maintaining species rich forests (Gil-Tena et al., 2007). For increasingly homogeneous forests, the creation and restoration of small forest openings by controlled logging and the promotion of traditional land uses such as extensive agriculture and low-intensity livestock grazing should show positive effects (Kati et al., 2009; Poirazidis et al., 2004, 2007). We recommend integrating landscape monitoring into forest management plans. This enhances sustainability and promotes the evaluation of effects of forest management on landscape and specific organismic groups. The metrics performed well for extents of 50 ha, which happens to be the average size of forest stands in Dadia NP (Poirazidis et al., 2011b). Landscape level metrics related to landscape diversity and patch shape could be applied as indicators of species richness for forest management plans that consider the conservation of biodiversity (Poirazidis et al., 2011b). For the optimal choice of metrics, case specific exploration of their indicator values is necessary. The present exploration provides a basis for the formal development of landscape structure indicators for forest landscape management and monitoring, and should promote further research regarding the indicator values of landscape metrics.

5. Conclusions

This study revealed clearly that landscape metrics can be a useful tool for the necessary integration of landscape approaches into conservation management. Regardless of the amount of open land versus forest, landscape diversity and landscape configuration proved to be related to species richness. Heterogeneous landscape mosaics of fine texture are crucial for the maintenance of biodiversity in seminatural Mediterranean forest ecosystems. Further key findings are that overall richness can be well indicated by several landscape level metrics, and that several of them are also good indicators for woody plants, orthopterans and reptiles. Species richness of orchids, on the other hand, is not easily predictable, while the poor performance of the metrics for amphibians and small terrestrial birds might be caused by particularities of the approach presented in this study. Scale has an influence on the indicator value of the metrics, which is generally better at smaller extents of surrounding landscape. Taxa with larger ranges and higher mobility seem to be affected by a wider extent of landscape than small and sedentary ones. To get a better picture of the underlying patterns and processes, we recommend further investigating and reviewing the consistency of the performance of landscape metrics as indicators of species richness along environmental gradients.

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