

COMPARING ENVIRONMENTAL AND BIOLOGICAL SURROGATES FOR BIODIVERSITY AT A LOCAL SCALE

YOHAY CARMEL* AND LIRON STOLLER-CAVARI

Division of Environmental, Water and Agricultural Engineering, Faculty of Civil and Environmental Engineering, Technion—Israel Institute of Technology, Haifa 32000, Israel

ABSTRACT

A recent debate concerns the relative merit of the two major types of surrogates for biodiversity, biological surrogates and environmental surrogates. Evidence, in the form of direct comparison of these two surrogate types, is scarce. We conducted a direct comparison of the performance of a series of biological and environmental surrogates, at a local scale (300 km²), which is often the relevant scale for land planning and management. Performance was referred to as the degree of surrogate congruence with a spatial pattern of diversity of woody species, of geophytes, and of land snails. “Environmental domains”, surrogates based on numerical classification of environmental variables (topography, soil, and vegetation cover), outperformed other environmental surrogates (qualitatively delineated vegetation units and physiographic land types). The environmental domains surrogates were robust to subjective decisions on a number of classes and on input variables that drove the classification. The best biological surrogate was the woody species diversity pattern, with performance similar to that of the environmental domains. Our results support the notion that environmental domains may be reliable and cost-effective surrogates for biodiversity at small scales, particularly in data-poor regions.

Keywords: biodiversity surrogates, environmental domains, *K*-means classification; protected areas, Mt. Carmel

INTRODUCTION

The entire range of biodiversity can never be fully mapped, and surrogate maps are used for conservation-oriented decision making (Belbin, 1993; Faith and Walker, 1996b). There are two major types of surrogates, biological and environmental. Biological surrogates are measures of richness, endemism, rarity, and complementarity of taxonomic or functional groups that are presumed to be indicators of biodiversity patterns at large (Prendergast et al., 1993; Gaston and Blackburn, 1995; Myers et al., 2000).

*Author to whom correspondence should be addressed. E-mail: yohay@technion.ac.il
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Environmental surrogates involve the partition of the land into spatial units, in which each unit is supposed to be relatively homogeneous in its environmental traits and different from other land classes (Mackey et al., 1989; Kirkpatrick and Brown, 1994). The rationale behind environmental surrogates is that environmental variation should indicate organismal diversity (Belbin, 1993; Faith and Walker, 1996a). Thus, congruence is expected between mapped land classes and the actual distribution of the myriad species that make up biodiversity. There are two distinct ways to delineate spatial boundaries between land classes: (1) qualitative classification of an area into land classes, based on information on soil properties, topography, or other land cover types (Cardillo et al., 1999; Oliver et al., 2004) or into vegetation types (Ferrier and Watson, 1997; Reyers et al., 2001), and (2) numerical classification of the land into environmental domains (Kirkpatrick and Brown, 1994; Fairbanks, 2000; Leathwick et al., 2003). In numerical classification of land, environmental layers (digital GIS maps of soil, topography, etc.) are used to classify the geographic space into spatial domains under explicit classification rules. The principal advantage of environmental domains is that they can be mapped remotely, providing full geographical coverage of large regions relatively cheaply and rapidly (Ferrier and Watson, 1997; Ferrier, 2002).

Criticism has been leveled at the biological-surrogates approach to biodiversity mapping (Franklin, 1993; Prendergast, 1997). Among the main problems are (1) the unknown, possibly large, cumulative error produced in the process of overlaying many species-distribution maps, where errors inherent in each data set are multiplied (Flather et al., 1997; Lenton et al., 2000); and (2) the low congruence between spatial patterns of diversity in different taxa (Lombard, 1995; Howard et al., 1998).

Most studies that have assessed the performance of environmental surrogates have yielded supportive results (e.g., Ferrier and Watson, 1997; Wessels et al., 1999; MacNally et al., 2002; Trakhtenbrot and Kadmon, 2005; see Table 1). Yet environmental surrogates have also received criticism, (1) because of low congruence between land classes and actual species distributions (Araujo et al., 2001, 2003; but see Faith, 2003, for another interpretation), and (2) because different weighting schemes of input variables and different classification procedures may yield entirely different environmental domains (e.g., Ferrier and Watson, 1997; MacNally et al., 2002; Trakhtenbrot and Kadmon, 2005).

Given the limitations of both surrogate types, a recent debate in the scientific literature concerns the merit of these surrogates, and which is most appropriate to use (Araujo et al., 2003; Faith, 2003; Brooks et al., 2004; Cowling et al., 2004; Pressey, 2004). This debate has little direct evidence to rely upon: although a fair number of studies have assessed the performance of surrogates for biodiversity (Table 1), most of them related to either biological or environmental surrogates. Surprisingly few studies compared the performance of both surrogate types directly (Kirkpatrick and Brown, 1994; Ferrier and Watson, 1997; Reyers et al., 2002; Bonn and Gaston, 2005). These studies used similar methods to compare surrogates. They assessed the proportion of area required to represent the same biodiversity elements using each surrogate (Kirkpatrick and Brown, 1994; Reyers et al., 2002; Bonn and Gaston, 2005). In these studies, both surrogate

types had some degree of success in representing biodiversity elements, and in all four studies neither surrogate type performed consistently and significantly better than the other (Kirkpatrick and Brown, 1994; Ferrier and Watson, 1997; Reyers et al. 2002; Bonn and Gaston, 2005). Environmental surrogates tended to miss rare species with a small distribution range (Kirkpatrick and Brown, 1994; Reyers et al., 2002). In some cases, environmental surrogates performed no better than expected by chance (Bonn and Gaston, 2005).

Most studies (Table 1) were conducted in relatively large areas, typically 10^4 – 10^6 km² (Table 1). One of the reasons for the scarcity of fine-scale studies is that both environmental and biological data are often available at coarse scales only. Yet, questions asked by local planners and managers typically address smaller areas (often at the scale of 10^2 – 10^3 km²; Kerr et al., 2000; Ferrier, 2002; Ricketts et al., 2002). Conclusions derived from coarse-scale studies may not hold at much finer scales (Rahbek, 2005). The typical use of environmental domains, the selection of a network of protected areas, is irrelevant at these small scales. Yet, local-scale environmental domains could prove particularly useful in delimiting the boundaries of a specific reserve and locating specific development projects. Our goal here is to compare directly the relative performance of biological surrogates and environmental surrogates in representing actual biodiversity patterns at a local scale.

METHODS

STUDY AREA

Mt. Carmel, Israel, typical of the Mediterranean region, provides a challenging scene for surrogates for biodiversity patterns owing to its fine-scale heterogeneity in topography, soil properties, and vegetation, and to the heavy human impact that confounds the impact of environmental determinants on species distributions. The study area was 330 km², with an altitude range of 40–520 m and annual precipitation between 600 and 770 mm.

BIOLOGICAL SURROGATES

We surveyed intensively three functional groups (woody species, geophytes, and land snails) across the entire region. Each group served as a reference to validate the two other biological surrogates and the environmental surrogates. We applied a strictly random sampling scheme in which 110 sites were distributed across the area (excluding urban areas and agricultural lands, Fig. 1). Site size was 0.1 ha. We recorded presence and absence data at three sample points within each site, with a distance of 20 m between sampling points. The sample area was 75 m² for woody species and geophytes and 1 m² for land snails. We surveyed plants and land snails from October 2002 through May 2003 and geophytes during March 2003. Yair Or of ROTEM, Israel Plant Information Center, and Henk Mienis of Tel Aviv University confirmed species identifications for plants and snails, respectively. We intentionally chose to use presence and absence data, in spite of the lower information content. The use of presence and absence data, as

Table 1
 Studies of surrogates for biodiversity. Surrogates for diversity patterns (species composition) were included, while surrogates for species richness per se were excluded. E—environmental surrogates, B—hybrids, E&B—both types in the same study, RSA—reserve selection algorithm

Type	Source	Surrogate	Land mapping	Representativeness assessment	Scale (km ²)
E	Araujo et al., 2001	Environmental domains	Numerical (PCA)	Representativeness of vertebrates and plants	10 ⁶
E	Belbin, 1993	Environmental domains	Numerical (ALOC)	None	10 ³
E&B	Bonn and Gaston, 2005	Environmental domains, birds	Numerical (ordination)	Effectiveness of hypothetical reserve network	10 ⁶
E	Burrough et al., 2001	Topo-climatic classes	Numerical (fuzzy <i>K</i> -means)	Congruence with vegetation cover classes	10 ⁴
E	Cardillo et al., 1999	Land use types	Numerical	Terrestrial mammals	10 ⁴
E	Fairbanks and Benn, 2000	Landscape ecosystems	Numerical	None	10 ⁴
E&B	Ferrier and Watson, 1997	Various environmental and biological surrogates	Numerical (classification, ordination) and qualitative	Various biological groups	10 ⁵
H	Ferrier et al., 2002	Environmental and species data	Numerical	10 biological groups	10 ⁴ –10 ⁵
E	Hilbert and Van Den Muyzenberg, 1999	Forest types	Numerical (neural network)	Vegetation types	10 ⁵
B	Howard et al., 1998	Woody plants, birds, mammals, moths, butterflies	None (RSA)	Cross-taxon congruence	10 ⁴
E	Kati et al., 2004	Orchids, woody plants, reptiles, birds, orthoptera	None (RSA)	Cross-taxon congruence	10 ²
B	Kerr et al., 2000	Lepidoptera	None	Lepidoptera as indicators for Hymenoptera	10 ⁴
E&B	Kintsch and Urban, 2002	“physical proxies”	None	Vascular plants	10 ³

E&B	Kirkpatrick and Brown, 1994	Environmental domains, endemic plants	Numerical and RSA	Representativeness: vegetation units, env. domains, endemic and rare species	10 ⁴
B	Lawler et al., 2003	Vertebrate classes and mussels	None	Against all species and against species at risk	10 ⁵
E	Leathwick et al., 2003	Environmental domains	Numerical	None	10 ⁵
E	Lombard et al., 2003	Land types	Qualitative	Protea, fish, amphibians, reptiles	10 ⁴
E	Lund and Rahbek, 2002	Seven taxa	None (RSA)	Cross-taxon congruence	10 ⁴
E	Mac Nally et al., 2002	Ecological vegetation classes	Qualitative	Birds, mammals, reptiles, trees, invertebrates	10 ⁴
E	Mackey et al., 1989	Environmental domains	Numerical (ALOC clustering)	Congruence with current reserve network	10 ⁴
B	Moore et al., 2003	Six vertebrate groups	None (RSA)	Each group indicates other groups	10 ⁷
B	Oertli et al., 2005	Bees, wasps, grasshoppers	None	Congruence: Cross-taxon and with land use types	10 ¹
E	Oliver et al., 2004	Land systems	Qualitative	Plants, invertebrates, micro-biota	10 ³
E&B	Reyers et al., 2002	Plants, mammals, birds, butterflies, vegetation types, land types	Qualitative	Various taxa	10 ⁵
B	Ricketts et al., 2002	Butterflies, moths	None	Butterflies as surrogates for moths and vice versa	10 ¹
E	Sarkar et al., 2005	Environmental domains	None (RSA)	Many plant and animal species	10 ⁶
E	Trakhtenbrot & Kadmon 2005	Environmental clusters	Numerical	Vascular plants	10 ⁴
E	Wessels et al., 1999	Land facets	Qualitative	Dung beetles, birds	10 ²

opposed to abundance data, decreases detectability of possible correlations between biological and environmental data sets because spatial patterns are less pronounced (Oliver et al., 2004). However, when such correlations are found, they are more likely to reflect profound biodiversity patterns than ephemeral patterns of abundance.

In order to construct biological surrogates compatible with the environmental surrogates (spatially explicit domains), we used species presence/absence data to classify the 110 sampling sites into 10 clusters (or classes, Ferrier et al., 2002). We chose *K*-means partitioning for this process (Legendre and Legendre, 1998). *K*-means partitioning is a least-squares nonhierarchical classification method that allows the user to divide a collection of objects into *K* groups (*K* is user-determined). In this procedure, each species is represented as an axis in an *n*-dimensional space (where *n* is the number of species). The Euclidean distance between sites in this space is used to classify these sites into classes. These biological classes allowed us to test the performance of each biological group as a surrogate for the two other groups, and for various environmental surrogates. This procedure was conducted separately for each of the three functional groups.

ENVIRONMENTAL SURROGATES

Qualitative surrogates. Two qualitative surrogates were evaluated, based on two existing maps of Mt. Carmel: (1) a map of physiographic units (Kaplan and Edelman, 1996; see Fig. 1), based mainly on topography, and (2) a map of vegetation units, (Lahav, 1983; see Fig. 2), based on a detailed field survey of woody species.

Numerically classified environmental domains. These surrogates are typically based on numerical classification of readily available digital GIS layers. Here, we used available GIS layers of Mount Carmel: soil maps, climate maps, topographic maps (DEM and its derivatives, slope and aspect maps), and a binary vegetation map (woody or herbaceous) derived from an aerial photo. We chose *K*-means partitioning (Burrough et al. 2001) to construct the numerical classifications (Fig. 3). We selected *K*-means partitioning over alternative classification methods because it can incorporate categorical variables, such as soil type, as well as continuous variables, such as elevation, without making assumptions about the statistical distribution of these variables. The user determines which variables are included in the iterative clustering process and the number of groups in the classification (here, the number of environmental domains in the map). Eight GIS layers were included in the classification: three climatic layers (mean daily temperature in January, mean daily temperature in August, and mean annual precipitation), three topographic layers (altitude, aspect, and slope), and two thematic layers (soils and vegetation cover). The vegetation-cover layer was derived from a supervised classification of a 1999 orthophoto of the region into two classes (woody or herbaceous). Pixel size in all layers was set to 25 × 25 m.

We constructed a basic surrogate that included 11 environmental domains and three groups of input variables (topography, vegetation, and soil properties; see Fig. 3). Next, we constructed two sets of surrogates, as modifications of the basic surrogate, to assess the robustness of environmental surrogates to subjective decisions on (1) input variable composition and (2) number of classes. Eight maps comprised the first set, which was

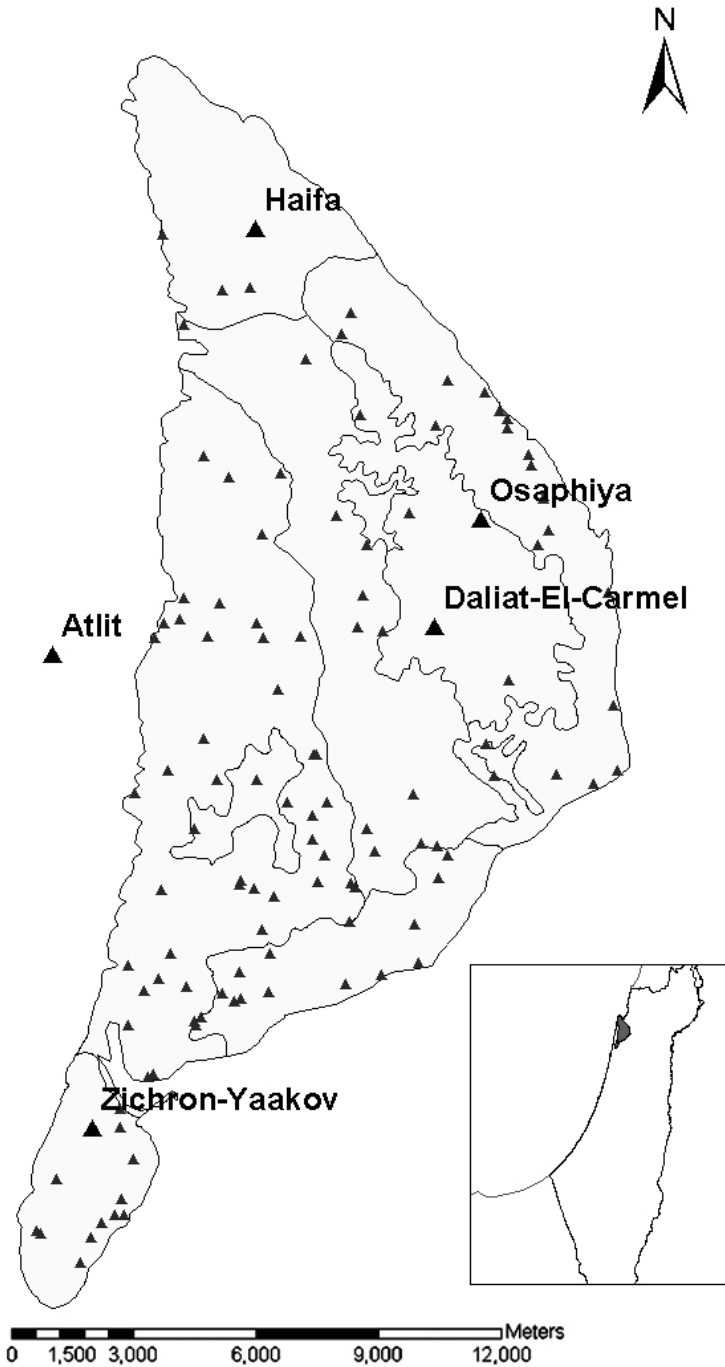


Fig. 1. Geographic units of the study area, Mt. Carmel, Israel. Polygons represent physiographic units. Triangles show sampling locations. Urban and agricultural lands were not sampled. Source: Kaplan and Edelman, 1996. Inset: Study area (shaded) on map of Israel.

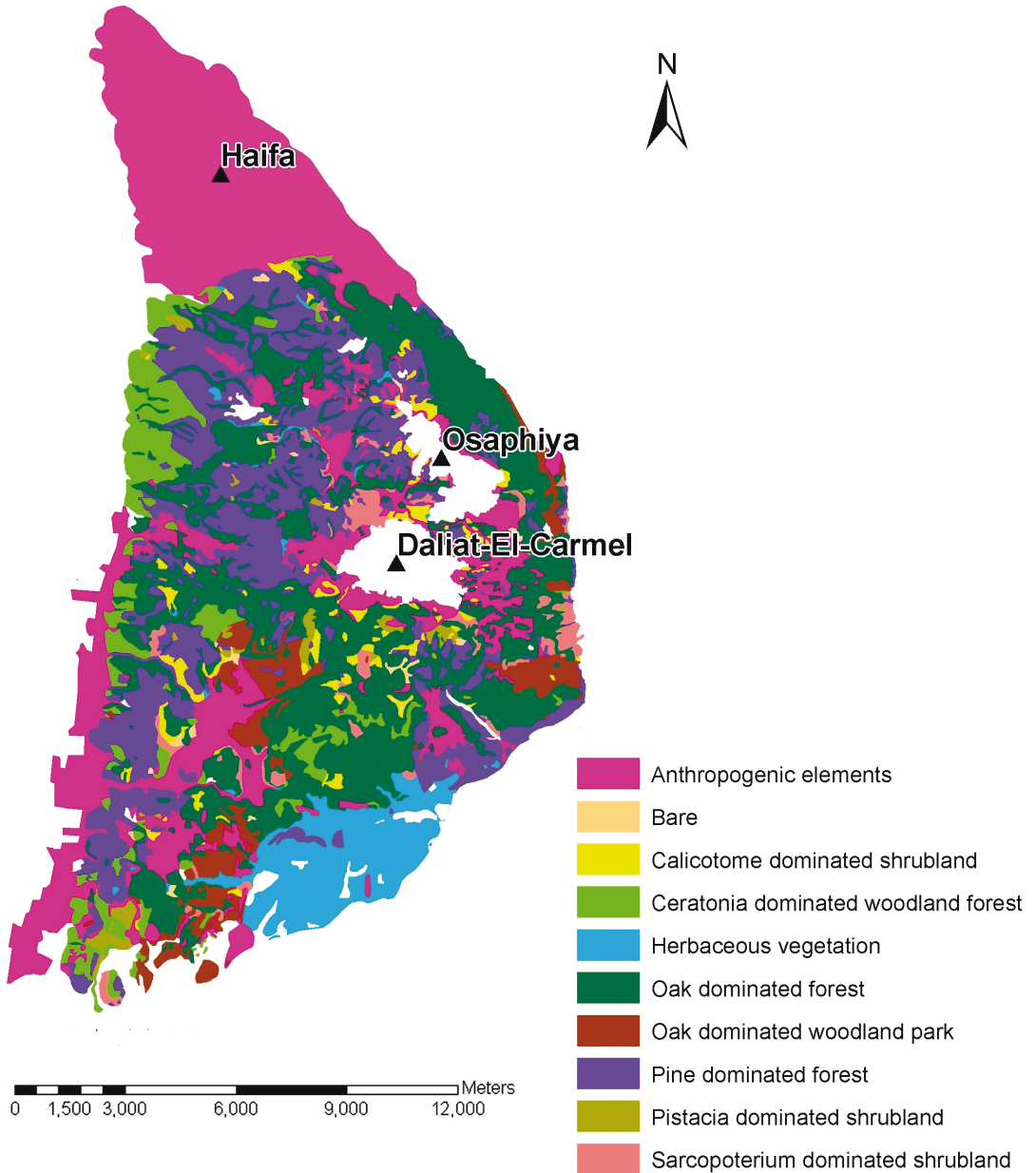


Fig. 2. Vegetation units map of the study area. After Lahav, 1983. The white areas, representing urban / built areas, were excluded from all analyses.

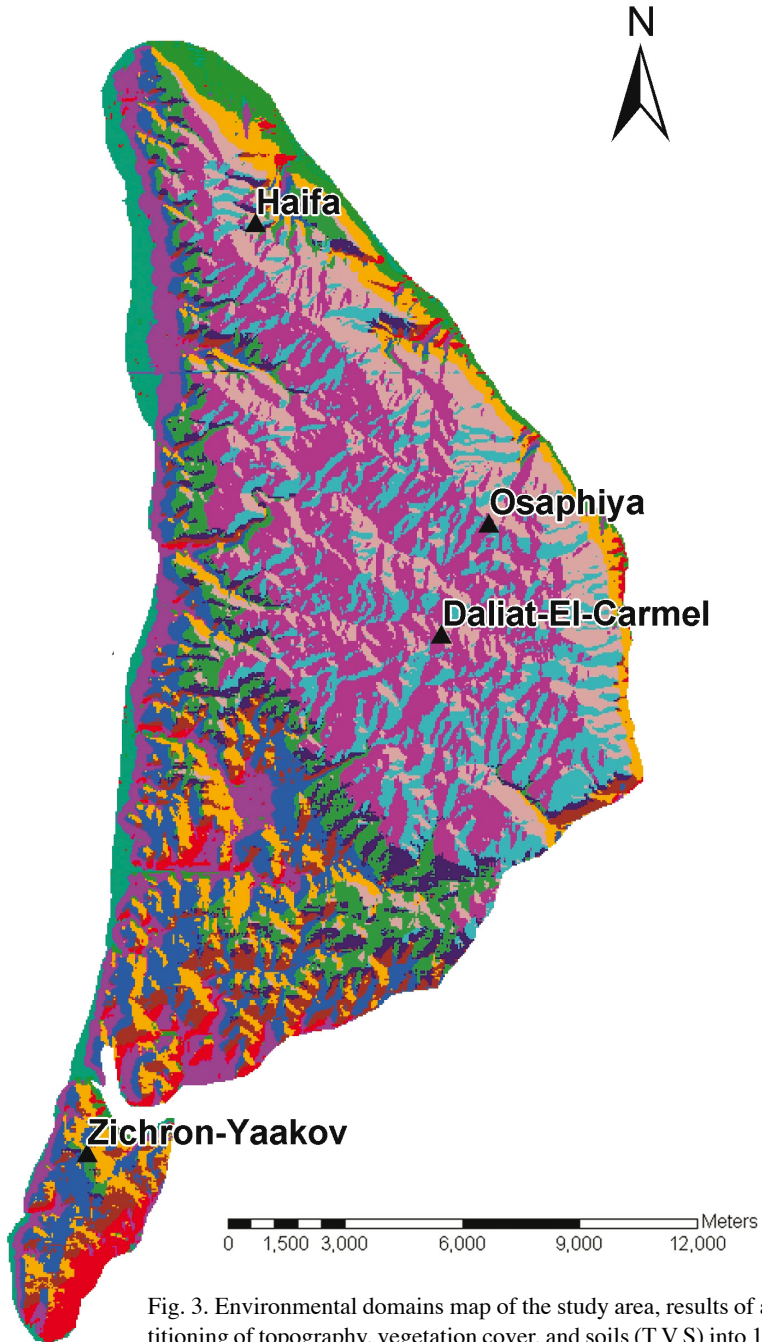


Fig. 3. Environmental domains map of the study area, results of a *K*-means partitioning of topography, vegetation cover, and soils (TVS) into 11 classes. Each class represents a unique combination of environmental parameters.

produced with different combinations of environmental variables in each classification. Thirteen maps comprised the second set, in which we varied the number of domains in each classification process (range 6–18) based on the same set of variables in all classifications.

SURROGATE PERFORMANCE

Surrogate performance was defined as the degree to which the particular classes in a surrogate correspond to specific species assemblages. Environmental surrogates were evaluated against each of the three biological groups. Each biological surrogate was evaluated against the two other biological groups. We used analysis of similarity (ANOSIM; Clarke, 1993) to test differences in species assemblages among surrogate classes for all the surrogates (both biological classes and land classes). If classes are different in their species composition, then compositional dissimilarities between the classes ought to be greater than those within the classes. ANOSIM is a nonparametric technique that allows formal comparisons of multivariate data sets similar to analysis of variance. This procedure uses the Sorenson similarity matrix to calculate R :

$$R = \frac{(r_{BETWEEN} - r_{WITHIN})}{0.25 \cdot n \cdot (n - 1)} \quad (1)$$

where r_{WITHIN} is the average of all rank similarities for samples within the same class, $r_{BETWEEN}$ is the average of all rank similarities for samples between different classes, and n is the total number of samples under consideration. Values of R near 1 indicate complete separation of sample groups, while values near 0 indicate no separation between groups.

In order to evaluate the significance of the R statistic, we applied a generalized permutation test (Legendre and Legendre, 1998; Manly, 1998): The rows and columns of the similarity matrix were randomly rearranged and the R statistic was recomputed for the new matrix. The distribution of R values was generated via many iterations (1000 iterations in our case for $\alpha = 0.05$; Manly, 1998). The permutation test allowed us to assess whether the observed pattern of similarities among classes (biological groups and land classes) is unlikely by chance alone. We performed ANOSIM tests for each of the environmental domains maps in order to assess the sensitivity of the classification to the number of classes and to various specific combinations of input variables in the classification process. The PRIMER software package (Clarke, 1993) was used for all ANOSIM calculations.

RESULTS

BIOLOGICAL SURROGATES

We found 56 species of woody plants, 52 species of geophytes, and 17 species of land snails. The highest richness for geophytes and woody species was on the eastern

slope of the mountain, and the lowest richness was on the southern, lower part of the mountain. Land snail richness had a somewhat opposite trend, with the highest richness on the southern part of the mountain. Woody species were good surrogates for both geophytes and land snails (Table 2). Geophytes were good surrogates for woody species, but not for land snails; land snails were not a good surrogate for either woody species or geophytes (Table 2).

ENVIRONMENTAL SURROGATES

The distribution of *woody species* among physiographic units was nonrandom (Table 2). In contrast, congruence between physiographic units and between both *geophytes* and *land snails* was insignificant. Similarly, the vegetation units were strongly associated with spatial patterns of woody species but not with those of geophytes and land snails (Table 2). The environmental domains (produced by numerical classification of environmental variables) were the only surrogate type that significantly reflected the patterns of all three functional groups (Table 2).

The numerically classified surrogates were robust to modifications in the composition of the input variables in the classification, for both woody species and geophytes. We constructed eight surrogate maps with various combinations of at least two of the four groups of input variables: vegetation (% woody vegetation); topography (slope, aspect, and elevation); climate (temperature, precipitation); and soil. ANOSIM R values and their respective p values varied relatively little between simulations with alternative compositions of variables, for woody species and geophytes (Table 2). For land snails, however, results were less consistent: five specific combinations yielded moderate or high values of congruence, while three other combinations yielded insignificant statistical values (Table 2).

When we modified the number of domains in the numerical classification, within the range of 6–18 domains, the resulting surrogate maps performed consistently well in reflecting diversity patterns of woody species. Congruence between these surrogates and geophytes was somewhat lower, and in two of thirteen cases it was only nearly significant. Congruence with land snail diversity patterns was more variable. Six surrogates were significantly congruent with land snail diversity patterns, while for four surrogates congruence with land snail diversity was nearly significant, and for three other surrogates it was insignificant (Table 2).

DISCUSSION

Our results revealed clear differences in performance between various surrogates of biodiversity. Biological surrogates: woody species were a good surrogate for the two other groups, geophytes corresponded to only one of the two other groups, while land snails did not reflect either of the other groups. Environmental surrogates: the qualitative surrogates (physiographic units and vegetation units) were good surrogates for woody species, but neither one reflected geophytes or land snails. The only environmental surrogate that successfully captured the patterns of all three biological groups was the map

Table 2

Congruence* between various biodiversity surrogates and spatial patterns of species diversity in three biological groups. Values are ANOSIM *R* statistic (*p* value). Cells with $0.10 > p > 0.05$ are in bold

		ANOSIM <i>R</i> statistic (<i>p</i> value)		
		Woody species	Geophytes	Land snails
Biological surrogates	Woody species		0.068 (0.022)	0.109 (0.003)
	Geophytes	0.072 (0.019)		0.046 (0.06)
	Land snails	NS	NS	
Environmental surrogates	Physiographic units	0.123 (0.013)	0.085 (0.054)	NS
	Vegetation units	0.348 (0.001)	NS	NS
	Env. domains	0.203 (0.001)	0.103 (0.001)	0.08 (0.005)
Combinations of input variables in <i>K</i> -means: T—topography V—vegetation S—soils C—climate	TV	0.203 (0.001)	0.079 (0.009)	NS
	VC	0.102 (0.003)	0.051 (0.042)	0.057 (0.045)
	TC	0.19 (0.001)	0.102 (0.001)	NS
	TVS	0.203 (0.001)	0.103 (0.001)	0.08 (0.005)
	TVC	0.151 (0.001)	0.056 (0.023)	0.073 (0.006)
	TSC	0.151 (0.001)	0.056 (0.026)	0.073 (0.008)
	VSC	0.148 (0.008)	0.141 (0.014)	NS
	TVSC	0.151 (0.001)	0.056 (0.021)	0.073 (0.013)
Number of clusters in the <i>K</i> -means classification	6	0.103 (0.001)	0.069 (0.002)	NS
	7	0.12 (0.001)	0.051 (0.019)	0.041 (0.069)
	8	0.163 (0.001)	0.074 (0.008)	0.043 (0.069)
	9	0.129 (0.001)	0.057 (0.016)	0.046 (0.06)
	10	0.175 (0.001)	0.045 (0.063)	NS
	11	0.203 (0.001)	0.103 (0.001)	0.08 (0.005)
	12	0.185 (0.001)	0.097 (0.003)	0.076 (0.007)
	13	0.214 (0.001)	0.081 (0.008)	0.093 (0.003)
	14	0.182 (0.001)	0.058 (0.04)	0.048 (0.082)
	15	0.276 (0.001)	0.077 (0.009)	0.043 (0.093)
	16	0.234 (0.001)	0.046 (0.054)	0.065 (0.002)
17	0.215 (0.001)	0.071 (0.022)	NS	
18	0.228 (0.001)	0.071 (0.031)	0.062 (0.05)	

*ANOSIM *R* statistic denotes degree of congruence between matrices of similarity between sampling sites, in species assemblages, and in environmental characteristics, respectively.

T—topography (slope, aspect, elevation), V—vegetation cover (either woody or herbaceous), S—soils, C—climate (precipitation, January temperature, and August temperature), NS—not significant.

of environmental domains produced using numerical classification of environmental variables. For woody species and geophytes this result was robust, consistent, and insensitive to the number of classes defined and to the specific composition of environmental variables in the classification. Land snails had a lesser degree of congruence with environmental domains and a variable response to changes in the number of domains and specific combination of input variables.

QUALITATIVE CLASSIFICATION VERSUS NUMERICAL CLASSIFICATION

Qualitative classifications generally aim to identify discrete units in geographic space and are therefore characterized by larger within-land-class environmental heterogeneity compared with numerically classified environmental domains. In contrast, numerical classification is based on similarity in a multidimensional environmental space. The resulting land classes are relatively homogeneous in their environmental traits but tend to be spatially irregular and fragmented (Fairbanks, 2000; Leathwick et al., 2003). These differences may explain the better performance of numerical classification, compared with qualitative classification, in representing diversity patterns of the biological groups studied.

Fine-scale maps of vegetation units have the potential to reflect the fine-scale environmental variation in structural features (Faith et al., 2001) or landform features (MacNally et al., 2002). This technique is a product of extensive field survey, so it is not surprising that patterns of woody species diversity were strongly reflected in this map. However, this map did not correspond to the spatial distribution of geophytes and land snails. Apparently, factors that affect distributions of these species were not represented in the classification, which was based on communities of woody species.

The *K*-means partitioning requires only two subjective decisions, namely, selecting input variables and determining the number of domains. Input variables are typically determined by data availability. No single number of domains is likely to be “optimal” in all situations (Belbin, 1993), and the choice is largely arbitrary. The numerical classification was insensitive to these two subjective decisions within a relatively wide range of values. For mapping environmental domains, the nonhierarchical nature of *K*-means partitioning may be a disadvantage; however, this problem can be solved by hierarchical clustering of domains, using the respective Euclidean distance between domain centers in the environmental space.

ENVIRONMENTAL DOMAINS AS SURROGATES

Numerically classified environmental domains significantly reflected the distribution patterns of the three biological groups studied, except for land snails in several cases. The lower performance for land snails may be attributed to the very small sampling unit (1 m² vs. 75 m² for the two other groups) and the smaller total number of species (17 vs. 56 and 52, for woody and geophyte species, respectively).

In our study, an environmental surrogate (environmental domains) and a biological surrogate (woody species) were the two best surrogates and performed similarly. The woody species diversity pattern was the best surrogate for land snails, while the envi-

ronmental domains map was the best surrogate for geophytes. This finding indicates that in certain situations, biological surrogates may outperform environmental surrogates in representing certain taxa. However, in data-poor regions, lack of resources for collecting biological data may preclude biological surrogates, while environmental surrogates may still be a viable option.

The link between underlying determinants of species diversity and environmental surrogates is scale- and taxon-dependent (Reyers et al., 2001, 2002; Ferrier, 2002; Ferrier et al., 2002). Here, the underlying determinants seemed to have been captured by numerically classified environmental surrogates that reflected diversity patterns of three biological groups at a local scale (300 km²). If these conclusions hold for other spatial scales, taxa, and regions, then it may turn out that the most time- and cost-effective method to map biodiversity is also one of its best surrogates.

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