

The relative dependence of Spanish landscape pattern on environmental and geographical variables over time

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Abstract

The analysis of the dependence of landscape patterns on environment was carried out in order to investigate the landscape structure evolution of Spain. The underlying concept was that the dependence between landscape spatial structure and environmental factors could be gradually decreasing over time. Land cover data were recorded from aerial photo interpretation of 206 4 × 4 km² samples from three different years: 1956, 1984 and 1998. Geographical variables were taken into consideration together with the purely environmental ones. General Linear Models of repeated measures were then used to segregate environmental from geographical effects on the pattern of the land cover patches of the samples. Aridity, lithology and topography were the environmental factors used to analyse structural indices of landscape.

Landscape composition has a higher dependence on environment than configuration. Environmental variables showed higher correlations with landscape composition and configuration than geographical variables. Among them, overall the climatic aridity and topography significantly accounted for more variation than did lithology.

There was a high degree of stability in land cover composition over time, with some significant exceptions. Nevertheless, the registered increase of fragmentation over time has demonstrated that configuration measures are needed to fully assess landscape change.

Key words: climatic effects, structural indices, landscape, composition, configuration, lithology, geography.

Resumen

Dependencia relativa entre los patrones de los paisajes españoles y variables medioambientales, geográficas y temporales

Se ha analizado la evolución de la estructura del paisaje español mediante un análisis de la dependencia de los patrones del paisaje respecto del medioambiente. La hipótesis principal es que la dependencia entre la estructura del paisaje y los factores ambientales está disminuyendo con el tiempo. Los datos de composición y configuración de paisaje fueron tomados mediante interpretación de fotografías aéreas tomadas en los años 1956, 1984 y 1998 en 206 parcelas de 4 × 4 km². Se han tenido en cuenta variables geográficas junto con las variables puramente ambientales. Se han utilizado modelos lineales generalizados de medidas repetidas para determinar la importancia de los efectos ambientales con respecto a los geográficos en los patrones de paisaje. Las variables ambientales utilizadas para analizar los índices estructurales del paisaje fueron: aridez, litología y topografía.

Existe una mayor dependencia ambiental en la composición que en la configuración. Las variables ambientales tuvieron un mayor efecto sobre la estructura del paisaje que las geográficas. Entre aquellas, la aridez climática y la topografía influyeron más que la litología. La composición se mostró en general estable a lo largo del periodo de estudio con algunas excepciones. Sin embargo, se observó una fragmentación significativa que indica la necesidad de analizar los índices de configuración para detectar los cambios de paisaje.

Palabras clave: efectos climáticos, índices de estructura, paisaje, composición, configuración, litología, geografía.

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Introduction

Landscape spatial pattern depends on environmental factors as well as on human actions (Forman & Godron, 1986), but the relative importance of such influences is not well known yet. It is generally accepted that primary environmental factors, such as air temperature and moisture regimes or soil types, are responsible for the development of the original vegetation cover. What it is not so clear is that they might also still be the most important factors in the development of current landscape patterns, because human activities have widely modified the initial cover and modulated these influences to a variable degree.

It is therefore important to know whether the human factors have over-ridden the original relationships between landscape pattern and the environment or they still remain. It is difficult to answer that question because many human actions that drive the landscape pattern, e.g. agricultural intensification and nitrogen deposition, could be simultaneously related to environmental variables, e.g. climate, bedrock and topographical factors. In fact, the human impact on non-forested rural lands in Europe is mainly determined by agricultural management and differs from region to region. In less rural areas, land cover involves industrial activities in which the associated management plays an important role as driving factor (Mander & Jongman, 1998).

It would also be useful to know the spatial and time scales at which the human factors act on landscape pattern. Local and regional knowledge of landscape structure, dynamics and function is a relevant issue not only for landscape ecologists, but also for conservationists and land use planners. Global and regional changes in land cover have taken place over long periods of time and have led to changes in environmental conditions and human population pressure (Turner *et al.*, 1990). On the other hand, local changes are mainly related to disturbances that take place over short periods of time and are heavily influenced by human activities.

As Naveh (2000) proposed, a landscape holistic approach rather than the consideration of individual elements in isolation is necessary for studying in depth the environmental and human influences on land cover dynamics. Landscape is conceptually defined as a system of ecosystems showing a well-defined spatial pattern, function and dynamics (Forman and Godron, 1986). In practice, landscape patterns consist of mosaics of land covers involving different land uses and types of semi-natural vegetation, as well as their spatial arrangement. Consequently, landscape pattern can be cha-

racterized by its composition and configuration (Dunning *et al.*, 1992). Landscape composition refers to the variety and abundance of patch types within a landscape. Landscape configuration refers to the shape and relative spatial placement of patches.

Our research has been carried out in the Spanish lands of the Iberian Peninsula and Balearic islands, an almost 500.000 km² country comprising a long history of human actions and a wide range of environmental factors. Spain is populated throughout, and the Iberian, Greek, Phoenician, Roman, Gothic, Muslim and Christian cultures have all left their footprints on its landscapes (Quezel *et al.*, 1977). Spanish rural landscapes are therefore one of the best examples in the world of long-lasting cultural interactions. The Mediterranean climate covers over 80% of Spain with Atlantic and Alpine climates in the north and west. The climatic stratification of Europe (Metzger *et al.*, 2005) defines five of the 13 European environmental zones in Spain. At the same time, Spain has a wide variety of bedrocks, as well as a wide range of elevations from sea level to over 3,700 meters. Thus Spain has a wide range of natural environmental regimes (Elena-Rosselló *et al.*, 1997) and is therefore especially suitable for studying the dependence of landscape pattern on environment.

The evolution of landscape in Spain considered as a whole has not been well studied, nor has the human impact on landscape, but there are several studies at the local level (Álvarez-Cobelas, 2007). Recently, rural Spanish landscapes have been monitored by the SISPAES system (Bolaños *et al.*, 2001) providing a vast database of their modern landscape pattern and dynamics. These data give us a unique opportunity to study the correlations between landscape pattern and both geographical and environmental factors.

Therefore, the main objective of the present paper is to analyse the dependence of landscape pattern (both composition and configuration) of Spain on the environment from 1956 to 1998, taking into account geographical variation. This analysis is relevant for knowing how and why landscape patterns have drifted from the original environmental constraints by the human influence.

Material and Methods

Stratified sampling design

Landscape composition and configuration was determined throughout Spain using a stratified random

network of samples based on primary environmental gradients. Sample analysis was carried out using aerial photos on a temporal series of square samples of 4×4 km² in the frame of the SISPARES project (Bolaños *et al.*, 2001). The samples are distributed on the Spanish Iberian peninsula and Balearic islands according to a geoclimatic land classification of Spain, called CLATERES as defined by Elena-Rosselló *et al.*, (1997). This classification was constructed by TWINSPAN multivariate analysis (Hill, 1979). Its design was based on a downwards nested classification analysis that assembles a bifocal dendrographic pattern and enables the classes to be used as a basis for a stratified field sampling (Barr *et al.*, 1993). This pattern also allows the upward grouping of neighbouring land classes into higher level categories for data analysis purposes (Smith, 1982). Any new class in the emerging level is the most significant union between the land classes existing in the previous lower level.

CANOCO ordination analysis (Ter Braak, 1987) was used to determine the primary environmental gradients using the mean climatic, altitudinal and lithological values and the relative presence of tree species into each geoclimatic class. The first axis expresses a climatic gradient from high to low aridity gradient. The second axis expresses a lithological gradient from basic to acid. The climatic gradient was divided into five levels to generate a geoclimatic class typology based on location of the main tree species (Elena-Rosselló *et al.*, 1997): A; Humid, B; Sub-humid, C; Sub-arid, D; Arid and E; Hyper-arid. Similarly, the lithological gradient was divided into three levels: 1; calcareous, 2; neutral and 3; siliceous. The distribution of 206 samples in these levels is shown in Figure 1A and B.

Landscape sample delineation

Each sample represents the landscape of one geoclimatic class and was analysed by delimiting patches of land cover and linear elements of road network from aerial photo interpretation. The scale of photos is 1:30.000 and the minimum patch size that it has been interpreted is 1 ha. The patches are relatively homogeneous portions of land that represent different land covers that are adjacent and make up the landscape. The typology of land cover used in this study, which derives from the CORINE land cover classification (EEA, 1995) is shown in Table 1. This analysis of landscape composition and configuration was made on photographs taken at three dates: 1956, 1984 and 1998. The last date photo-interpreted was validated by means of field visits.

One 4×4 km² area per class was chosen as a suitable size of landscape sample based on two requirements. Firstly, the maximum size that could be contained in the smallest geoclimatic class and secondly, a constant size for all landscapes as a means for calculating consistent landscape configuration indices and to examine the relative roles of different environmental variables (Whittaker *et al.*, 2001). This sample size has been generally used in landscape monitoring studies (Honnay *et al.*, 2003). The intensity of sampling, taking into account sample size and the area of the national territory, is around 1/146.

Spatial analysis of landscape samples

The ageneral use of several composition and configuration indices in scientific research demonstrates that

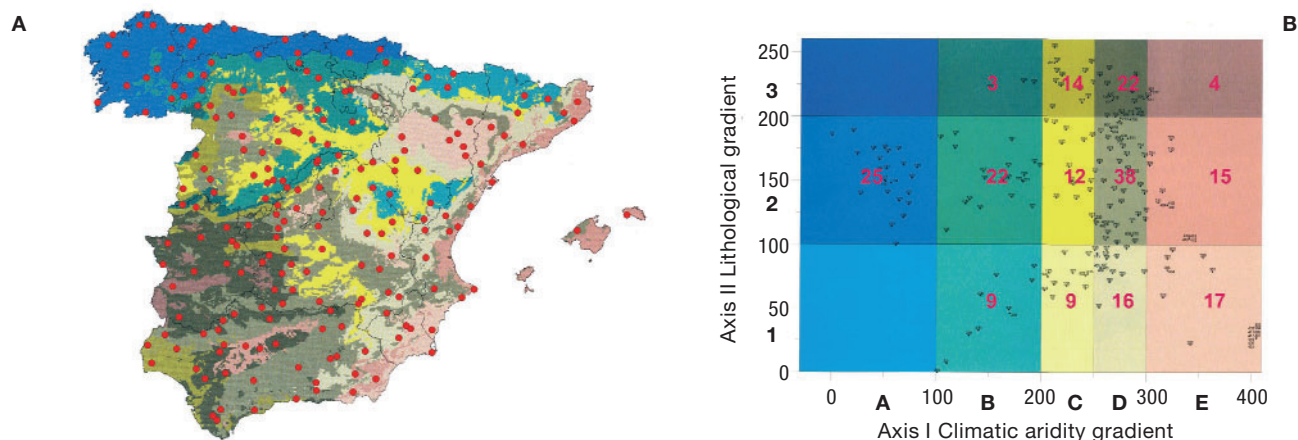


Figure 1. A: Map of Spain with the location of 206 samples of the SISPARES network used to analyse landscape composition and configuration. B: Distribution of 206 samples in two environmental gradients, climatic aridity and lithology.

Table 1. Types of land cover detected by interpretation of aerial photographs and their correspondence with land cover CORINE classification

Type of land cover	CORINE/level
Forest	Forest/3.1
<i>Matorral</i>	Shrub and/or herbaceous vegetation associations/3.2
<i>Dehesa</i>	Agro-forestry areas/2.4.4
Forest plantation	Young Broad-leave forests/3.1.1. and Young Coniferous forests/3.1.2
Pastures	Pastures/2.3.1
Crops	Arable land/2.1 and permanent crops/2.2
Riparian woodland	Riparian woodland/3.1.1.5
Rock	Bare rock/3.3.2
Water body	Water bodies/5.1.2
Urban and industrial use	Artificial surfaces/1

Source: EEA, 1995.

a single index cannot adequately characterize landscape spatial structure (Mc Garigal *et al.*, 1995). Early studies on landscape spatial analysis used a small list of indices in order to describe different subjects in a simple way (Turner & Gardner, 1991). However, a more useful strategy is to select indices by means of clustering based on correlations. Some studies indicate the suitability of indices for each spatial scale (Riitters *et al.*, 1995; Eiden *et al.*, 2000).

The landscape composition indicators used were ten land cover types (Table 1) and two land cover type diversity indices (Table 2). Only six of ten land cover types that were detected by photo-interpretation in 1956, 1984 and 1998 have been used in the model because of their relevance, being present in some samples with percentages higher than 50%. These cover types were: forest, forest plantation, *dehesa*, *matorral*, crops and pastures. The percentage of total area occupied by the other four land cover types (urban, rock, water body and river bank) was very low (far below 5%) in any landscape sample.

The eleven landscape configuration indices used are shown in Table 2. These indices were classified by means of a *1-Pearson r* cluster (Fig. 2). The only variables selected were MNN, LPI, DC, MPE, IJI, MSI, MPFD and PD. MPAR was not selected because it was highly related to MPFD (*1-Pearson r* = 0.10). Similarly, ED and SHPI were excluded for their relationship to PD (*1-Pearson r* = 0.14 and 0.18, respectively).

These eight landscape configuration indices and the eight landscape composition indices were used as dependent variables to build models having geographical and environmental variables as independent factors.

Data analysis

The assessment of the dependence of landscape pattern (composition and configuration) on environment must take geographical variables into account because their relationship may be masked by these variables. Moreover, the use of geographical variables will incorporate the effects caused by historical variables (Legendre & Legendre, 1998). In order to separate environmental effects from geographical effects, partial regression analysis has been used to assess the response variables variation into a *Purely Environmental fraction* (PE), a *Geographical Structured Environmental fraction* (GSE) and a *Purely Geographical fraction* (PG) (Borcard *et al.*, 1992; Legendre 1990, 1993). The total variation is the addition of these fractions plus an undetermined variation (Legendre & Fortin, 1989). In order to explain temporal changes in landscape composition and configuration, significant temporal variation has been included in the total variation of the response variable with a repeated measurement procedure.

The geographical parameters were calculated by regression of the response variables using the following third-degree polynomial of the central longitude (X) and latitude (Y) of each sample (Legendre, 1993): $b_1X + b_2Y + b_3X*Y + b_4X^2 + b_5Y^2 + b_6X^3 + b_7Y^3 + b_8X^2*Y + b_9X*Y^2$.

Longitude and latitude have been centred on their respective means prior to submitting the nine terms of polynomial to a backward selection procedure to remove the non-significant geographical terms as Legendre & Legendre (1998) recommended.

The method of regression analysis has been General Linear Models with repeated measures (GLM) (Snedecor & Cochran, 1980). These types of models use the least square methods to estimate and test hypotheses about

Table 2. List of indices used to describe landscape composition and configuration of Spain by means of 4×4 km² size units. PR and SDI are landscape composition indices and the rest are configuration indices. They have been computed by FRAGSTATS version 3

Name	Description	References
Landscape richness index (PR)	Number of types of land cover present per sample. Also termed Patch Richness	McGarigal and Marks (1995), Eiden <i>et al.</i> (2000)
Landscape diversity index (SDI)	Evenness of land covers per sample, calculated using the Shannon formula	Eiden <i>et al.</i> (2000)
Landscape fragmentation index (PD)	Number of patches per sample. Also termed Patch Density (number/100 ha)	McGarigal and Marks (1995) and Eiden <i>et al.</i> (2000)
Patch Size Diversity Index (SHPI)	Evenness of patch size per sample, calculated using the Shannon formula	McGarigal and Marks (1995)
Edge Density (ED)	Total length of edges per sample area (m/ha)	Eiden <i>et al.</i> (2000)
Mean Patch Fractal Dimension (MPFD)	Fractal dimension is twice the logarithm of patch perimeter (m) divided by the logarithm of patch area (m ²)	McGarigal and Marks (1995)
Mean Nearest Neighbour (MNN)	Mean of the Nearest Neighbour distances that is the shortest distance to a similar patch (centre to centre)	McGarigal and Marks (1995)
Interspersion and Juxtaposition index (IJI)	A measure of the interspersion of each patch in the sample	McGarigal and Marks (1995)
Largest Patch Index (LPI)	Area of the largest patch in the sample (%)	McGarigal and Marks (1995)
Mean Patch Edge (MPE)	Average amount of edge per patch	McGarigal and Marks (1995)
Mean shape Index (MSI)	Sum of the perimeter of each patch divided by the square root of patch area (ha) for all patches, divided by the number of patches	McGarigal and Marks (1995)
Mean Perimeter Area ratio (MPAR)	Mean ratio of the patch perimeter (m) to area (m ²)	McGarigal and Marks (1995)
Net road density (RD)	Km of road per sample	

Source: McGarigal and Marks, 1995.

effects and allow the analysis of designs with any combination of categorical independent variables, e.g. the climatic aridity and lithology gradients, continuous predictor variables, e.g. topographic and geographical as well as repeated measures over time.

Four topographic variables have been tested: minimum, maximum, mean and range altitude of 25×25 m grid cells per sample. A linear, quadratic or cubic function of topography variables was selected by comparing their explained variance. Only the variable that explained the most total variance was selected as an environmental variable to avoid colinearity. As a first step, the selected topographic variable and other environmental variables, climate and lithology, were regressed by using the forward method including the interaction terms. As a second step, the third-degree polynomial of longitude (X) and latitude (Y) of each sample was

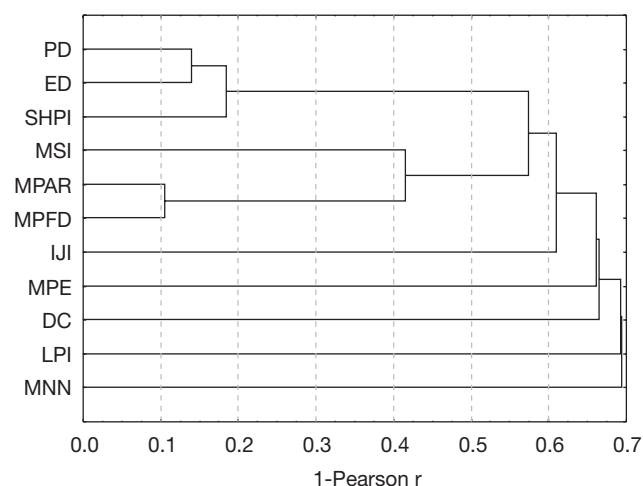


Figure 2. Dendrogram of cluster analysis of 11 landscape configuration indices by 1-Pearson r statistic. Acronyms of indices are decrypted in Table 2.

analysed through regression processing. As a third step, the remaining statistically significant environmental and geographical variables ($p > 0.05$) were analysed by using the regression forward method including the interaction terms sequentially one by one from the previous model. Percentage of land cover types was log-transformed to approximate to normalise variable distributions and to minimize deviances from normal distribution patterns caused by skewness. All statistical computations were carried out by means of the STATISTICA package (1999).

Results

Geographical and environmental determinants of landscape composition of Spain

The explained variance by environmental and geographical variables displayed in Table 3 and Table 4 corresponds to the *Purely Environmental* (PE) or *Purely Geographical* (PG) fractions plus the *Geographical Structured Environmental* fraction (GSE). Thus to calculate the Purely fractions it is necessary to subtract the GSE fraction, as shown in Table 5.

Altogether environmental and geographical variables have explained land composition from 41% (*matorral*) to 20% (forest plantation) of the total variance (Table 3). Consequently, the remaining unexplained variation is ranging from 59 until 80 % of the total variance.

Environmental variables explained more variance than geographical variables for the majority of land cover types, explaining almost 30% of the total variance, with the exception of *dehesa*, forest plantation and pastures as shown in Table 3. These land cover types have exhibited a high GSE fraction indicating a restricted distribution, which overrides the impact of purely environmental variables (Table 5). The aridity gradient explained the distribution of forest plantations and pastures in the Humid level, forest in Sub-humid level, *dehesa* in Sub-arid and Arid levels and crops in Arid level. *Matorral* distribution was not explained by the aridity gradient because this landscape type was widespread on all climatic and lithological levels (Fig. 3A, B, C). The lithological gradient explained the distribution of forest and crops land cover types in calcareous level, *dehesa* in siliceous level and pastures in neutral and siliceous level (Fig. 3B). Topographic variables explained that the forest land cover type was mainly distributed between 1,100 m and 1,500 m asl,

dehesa at altitudinal maximum of 500 m asl, crops at low elevation ranges and *matorral* at medium ranges (Fig. 4A).

Geographical variables explained the predominant position of forest land cover type in the north-east of Spain. Significant interactions between time and climate levels, longitude and latitude (Table 3) and a low GSE fraction (Table 5) were also found, denoting a widespread distribution of this land cover type. *Dehesa* is mainly located in the west of Spain, forest plantations in the north and pastures in north-west (Table 3). *Matorral* and crops showed the smallest geographical effects because they are present throughout Spain. Many significant interactions between variables were detected in both land cover types, also indicating a general distribution (Table 3).

Temporal variation has been significant in models of forest plantation, *matorral* and crops land cover type. A 400% increase of forest plantation total area was detected between 1956 and 1984, as a consequence of the reforestation policy in Spain in that period, but this area remained stable by 1998 (Fig. 3C). However, the percentage of crops and *matorral* per sample decreased from 1956 to 1984 and no significant temporal variation was recorded in *dehesa* and pastures land cover type over time.

Diversity indices of landscape composition decreased along the climatic aridity gradient (Fig. 3D). Patch Richness (PR) increased with time and showed a curvilinear relationship with minimum altitude because of an increase at middle altitudes (Fig. 4B). PR was high in the north-west of Spain (Table 3), but the explained variance of total models was low and decreased with time from 21% in 1956 to 10% in 1998. The Shannon landscape diversity index (SDI) increased with altitudinal range in a curvilinear relationship (Fig. 4B). Environmental effects explained more variance on SDI than on PR, but geographical effects were lower.

Environmental and geographical determinants of landscape configuration in Spain

The explained variance in all models of landscape configuration indices was lower than in landscape composition models, with the exception of the model for road network density (RD) that had explained a variance of 34% (Table 4). The effect of geographical variables on the configuration indices was lower than that of environmental variables, or non significant.

Table 3. Modelling the percentage of area per sample ($4 \times 4 \text{ km}^2$) occupied by land covers and landscape richness and diversity with General Linear Models of repeated measures. Significant effects of environmental, geographical and temporal factors are expressed as follows

Landscape composition indicator	Model	D.F.	F-value			% explained variance		
			1956	1984	1998	1956	1984	1988
<i>Forest</i>								
Environmental	L+MEAN+MEAN2-MEAN3+T*C	171	6.9***	6.5***	5.7***	0.27	0.26	0.23
Geographical	X+Y-Y3-T*X*Y2	176	10.2***	9.3***	7.5***	0.19	0.17	0.15
Total	L+MEAN2-MEAN3+X+Y-Y3+C*Y	173	9.8***	9.3***	7.7***	0.39	0.38	0.33
<i>Forest plantation</i>								
Environment	C+T	123	10.5***	8.1***	7.2***	0.25	0.21	0.19
Geographical	Y2+Y3+T	125	18.4***	14.6***	10.1***	0.23	0.19	0.15
Total	C+Y2+T	122	8.9***	7.3***	6.3***	0.27	0.23	0.20
<i>Dehesa</i>								
Environment	L+MAX-MAX2+MAX3	72	3.8**	4.1**	4.6**	0.21	0.22	0.24
Geographical	-X-X2-Y-Y2	73	3.9**	4.5**	5.8***	0.17	0.20	0.24
Total	C+L+MAX-MAX2+MAX3-X2	67	4.1***	4.1***	3.6***	0.38	0.38	0.35
<i>Matorral</i>								
Environment	RANGE-RANGE2	193	41.0***	37.9***	36.0***	0.30	0.28	0.27
Geographical	X-X*Y-X3+T	192	4.7**	3.5*	5.2**	0.07	0.05	0.07
Total	RANGE-RANGE2+X-X3-RANGE*X-C*X-C*Y+T	182	8.7***	9.0***	9.9***	0.38	0.39	0.41
<i>Crops</i>								
Environment	C+L-RANGE+T*C+T*RANGE	186	11.3***	16.9***	17.0***	0.30	0.39	0.39
Geographical	X-X2-X*Y2+T	190	5.4**	3.7*	4.2**	0.08	0.06	0.06
Total	L-RANGE+X-X2-X*Y2+T*C+T*RANGE	183	9.6***	12.6***	13.0***	0.35	0.41	0.42
<i>Pastures</i>								
Environment	C+L	188	10.8***	12.3***	12.6***	0.26	0.28	0.29
Geographical	-X+Y2+Y3	191	17.2***	18.7***	24.9***	0.21	0.23	0.28
Total	C-X+L*Y	187	9.9***	11.5***	11.6***	0.27	0.30	0.30
<i>Patch richness</i>								
Environment	C-MIN3+T+T*C	200	7.8***	2.3*	3.2**	0.16	0.05	0.07
Geographical	-X+Y+T-T*X*Y+T*Y+T*Y2-T*Y3	200	9.0***	4.0**	2.2	0.18	0.09	0.05
Total	-X*Y-MIN3+T-T*X*Y+T*Y2	195	5.2***	2.3*	2.1*	0.21	0.11	0.10
<i>Shannon diversity</i>								
Environment	C+RANGE-RANGE2+RANGE3+T*L+T*RANGE+T*RANGE2	196	9.3***	10.7***	10.1***	0.30	0.33	0.32
Geographical	X2-X*Y+T*X2*Y	197	2.4*	3.0**	2.7**	0.09	0.11	0.10
Total	C+RANGE-RANGE2+RANGE3+C*X+T*C+T*RANGE	194	9.5***	12.1***	11.0***	0.35	0.41	0.38

C: climate. L: lithology. MIN, MAX, MEAN and RANGE indicate minimum altitude, maximum altitude, mean altitude and altitudinal range, respectively, X longitude and Y latitude, and T time. Total is the final model that included significant environmental, geographical factors and significant interactions. All landscape composition indicators has been log transformed before modelling to avoid high skewness. Significant level less than 0.5, 0.01 and 0.001 is indicated by *, ** and ***, respectively.

Table 4. Modelling of the landscape configuration indices with General Linear Models of repeated measures. Significant effects of environmental, geographical and temporal factors are expressed as follows

Landscape configuration index	Model	D.F.	F-value			% explained variance		
			1956	1984	1998	1956	1984	1988
<i>RD</i>								
Environment	C+L-MAX+T+T*C+T*L	198	12.4***	13.7***	13.8***	0.30	0.33	0.33
Geographical	X*Y2+T+T*X*Y2	204	14.9***	0.4	1.4	0.07	0.00	0.01
Total	C-MAX+T+T*L+T*X*Y2	197	10.9***	12.7***	12.6***	0.31	0.34	0.34
<i>MPE</i>								
Environment	C+T	201	2.6*	2.9*	1.6	0.05	0.05	0.03
Geographical	Y+T	204	15.1***	11.8***	10.9**	0.07	0.05	0.05
Total	C+Y+T	200	4.2**	4.3**	3.1**	0.09	0.10	0.7
<i>MPFD</i>								
Environment	C+T+T*C	201	4.6**	2.4	1.0	0.08	0.05	0.02
Geographical	Y+T	204	2.6	7.2**	7.6**	0.01	0.03	0.04
Total	C+T+T*C+T*Y	197	3.1**	2.1*	2.1*	0.11	0.08	0.08
<i>MNN</i>								
Environment	L-RANGE+RANGE2	201	2.1	2.6*	4.6**	0.04	0.05	0.08
Geographical	-X	204	12.4***	8.3**	6.6*	0.06	0.04	0.04
Total	-RANGE+RANGE2-X	202	5.6**	4.6**	4.9**	0.08	0.06	0.08
<i>LJI</i>								
Environment	C+RANGE-RANGE2+RANGE3	199	2.7*	4.2***	4.0***	0.09	0.13	0.12
Geographical	Y3	204	3.1	9.5**	7.2**	0.01	0.04	0.03
Total	RANGE-RANGE2+RANGE3+ +RANGE*Y	201	4.5**	5.2***	4.0**	0.08	0.09	0.07
<i>PD</i>								
Environment	C+L+RANGE-RANGE2+RANGE3+T+ +T*C+T*RANGE	196	3.4***	3.6***	5.2***	0.14	0.14	0.19
Geographical	Y+T	204	14.6***	18.1***	19.0***	0.07	0.08	0.09
Total	RANGE-RANGE2+RANGE3+Y+T*C+ +T*RANGE	197	3.6***	5.3***	6.4***	0.13	0.18	0.21
<i>LPI</i>								
Environment	C-RANGE+RANGE2-RANGE3	198	5.6***	7.5***	7.1***	0.16	0.21	0.20
Geographical	X*Y+T	204	8.7**	12.6***	8.4**	0.04	0.06	0.04
Total	C-RANGE+RANGE2-RANGE3+C*X	194	5.6***	7.2***	6.7***	0.24	0.29	0.27
<i>MSI</i>								
Environment	T*C+T*RANGE	200	2.2*	1.0	0.7	0.05	0.03	0.02
Geographical	-X*Y+T+T*X*Y	204	0.7	7.3**	3.5	0.00	0.03	0.02
Total	T*C+T*RANGE-X*Y	199	2.2*	2.0	1.4	0.06	0.06	0.04

C: climate. L: lithology. MIN, MAX, MEAN and RANGE indicate minimum altitude, maximum altitude, mean altitude and altitudinal range, respectively, X longitude, Y latitude and T time. Total is the final model that included significant environmental, geographical factors and temporal variation and significant interactions. Significant level less than 0.5, 0.01 and 0.001 is indicated by *, ** and ***, respectively. The meaning of acronyms of landscape configuration indices is given in Table 2.

Table 5. Total percentages of explained variance of landscape composition and configuration indices from partial regression analysis of Tables 3 and 4 separating the response variable variation into a purely environmental fraction (PE), a geographically structured environmental fraction (GSE) and a purely geographical fraction (PG)

Landscape indices	1956			1984			1998		
	PE	GSE	PG	PE	GSE	PG	PE	GSE	PG
Forest	0.20	0.07	0.12	0.21	0.05	0.12	0.18	0.05	0.10
Forest plantation	0.04	0.21	0.02	0.04	0.17	0.02	0.05	0.14	0.01
<i>Dehesa</i>	0.06	0.15	0.02	0.08	0.14	0.06	0.04	0.20	0.04
<i>Matorral</i>	0.28	0.02	0.05	0.28	0.00	0.05	0.25	0.02	0.05
Crops	0.27	0.03	0.05	0.35	0.04	0.02	0.36	0.03	0.03
Pastures	0.06	0.20	0.01	0.07	0.21	0.02	0.02	0.27	0.01
Land cover Richness	0.03	0.13	0.05	0.02	0.03	0.06	0.05	0.02	0.03
Land cover Shannon Diversity	0.26	0.04	0.05	0.30	0.03	0.08	0.28	0.04	0.06
RD	0.24	0.06	0.01	0.33	—	n.s.	0.33	—	n.s.
MPE	0.02	0.03	0.04	0.05	0.00	0.05	0.02	0.01	0.04
MPFD	0.08	—	n.s.	n.s.	—	0.03	n.s.	—	0.02
MNN	0.02	0.02	0.04	0.02	0.03	0.01	0.04	0.04	0.00
IJI	0.06	0.03	0.00	0.07	0.06	0.00	0.06	0.06	0.00
PD	0.07	0.07	0.00	0.10	0.04	0.04	0.12	0.07	0.02
LPI	0.12	0.04	0.00	0.15	0.06	0.00	0.16	0.04	0.00
MSI	0.05	—	n.s.	n.s.	—	0.03	n.s.	—	n.s.

The aridity gradient explained high values of RD and Patch Density (PD) in its two extreme values. High values of Largest Patch Index (LPI) and Interspersion and Juxtaposition Index (IJI) are reached in Hyper-Arid and Humid levels, respectively (Fig. 5A, C, E). The lithological gradient only explained the high values of Mean Neighbour Distance (MNN) in siliceous level, RC in neutral level and PD in calcareous level (Fig. 5B, D). Mean Patch Fractal Dimension (MPFD) was not linked to lithological gradient in GLM model, but in Fig. 5B can be observed that MPFD is high in calcareous level. Probably, the temporal variation minimizes the effect of lithology. Topographic variables predict high values of RD in a low altitudinal maximum, high PD in mid-altitudinal ranges, high LPI in low-altitudinal range and high MNN in altitudinal ranges of 200 m and higher than 1,000 m. In this last case (MNN) a curvilinear relationship was found (Fig. 6A, B). Geographical variables indicate high values of MNN in the west of Spain, high LPI in the south-west and high PD in the north (Table 4). Temporal variation of configuration indices only has been significant in RC, MPFD and MPE (Fig. 5A, C). RC and MPFD increased over time and MPE decreased. PD and MSI had significant interaction between time and environmental variables that minimize the temporal variation, which results in an increase over time (Fig. 5E).

Correspondence between landscape composition and landscape configuration

Table 6 shows the landscape configuration and composition indices that were highly correlated. LPI was negatively correlated with the percentage of *matorral*, pastures and forest plantation and positively correlated with crops and *dehesa*. PD was positively correlated with *matorral*, pastures and forest plantation and negatively with *dehesa*. Both configuration indices indicate the different way of territory occupancy of those land cover types. There was a positive correlation of crops with RD and MPFD as well as a high negative correlation between crops and landscape diversity ($r = -0.53$; $p < 0.01$), showing the impact of cultivation and a pattern common to western and central Europe. RD was also correlated positively with forest plantation and negatively with forest, *dehesa* and *matorral*, as well as MPFD. IJI was positively correlated with forest, pastures and forest plantation and negatively with crops, indicating the different grade of patch mixing in agricultural and forest land cover types. MPE, MNN and MSI were landscape configuration indices that evinced low correlation with land cover types. Landscape composition as measured by SDI and PR was positively correlated with PD and IJI, but negatively correlated with LPI and MPE (Table 6).

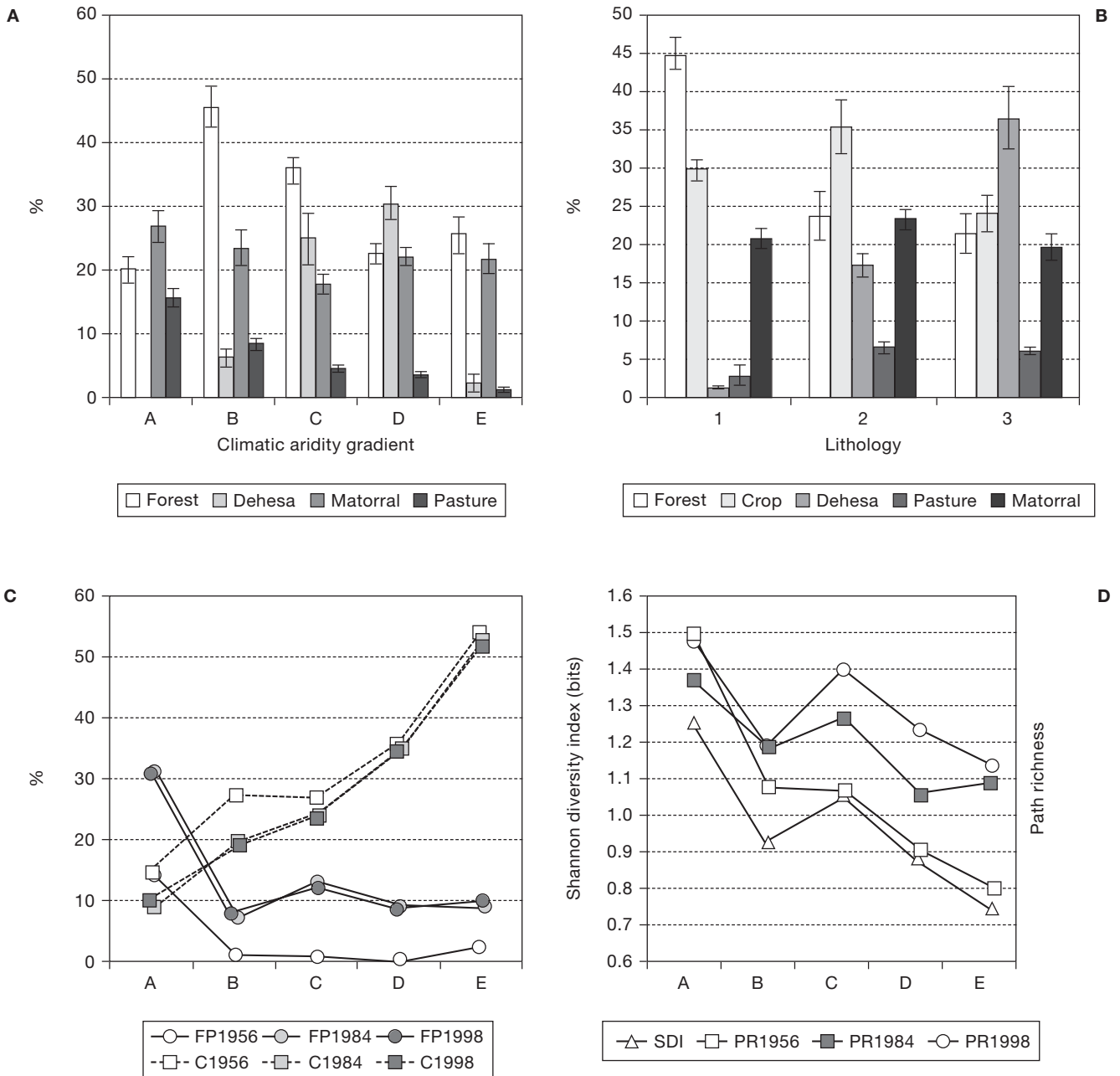


Figure 3. Relationships between landscape composition indicators and two environmental gradients. Mean percentage of area per sample occupied by some land covers in relation with (A) climatic aridity gradient and (B) lithology gradient. C: Temporal variation of mean percentage of area per sample occupied by forest plantation (FP) and crops (C) in relation with climatic aridity gradient. D: Mean Shannon Diversity Index (SDI) and temporal variation of mean Patch Richness (PR) in relation to the climatic aridity gradient. Ascendent sorted dates are indicated by increase of symbol size in (C) and (D).

Discussion

The analysis of spatial and temporal changes in composition and configuration of representative Spanish rural landscapes has shown significant

relationships with environmental and geographical variables. These relationships indicate different degrees of environmental dependence of the main land cover types and landscape configuration indices.

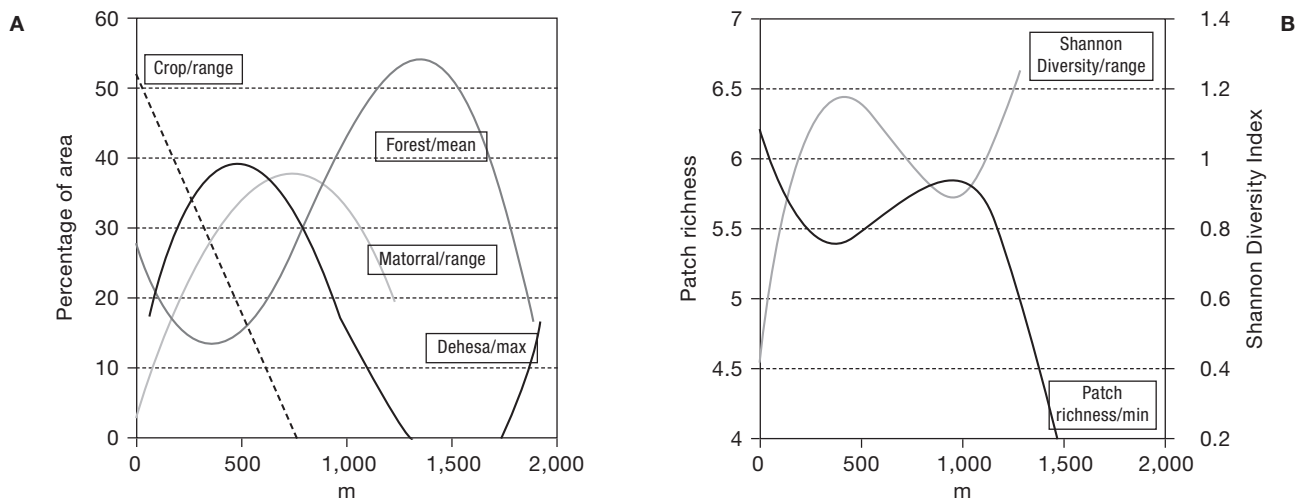


Figure 4. Relationships between landscape composition indicators and topographic variables as a result of GLM fittings. A: Percentage of area per sample occupied by some land covers in relation to altitudinal Range, Mean, and Maximum. B: Patch Richness (PR) and Shannon Diversity Index (SDI) in relation to altitudinal Minimum and Range, respectively.

Determinants of landscape composition and configuration

The relationship of landscape composition and configuration with environment can be over-ridden by the geographical location, e.g. longitude and latitude of a given landscape, because these variables are a major source of false correlations (Legendre & Legendre, 1998). Partial regression analysis using geographical variables has helped to limit the interference of such correlations by removing large-scale trends from environmental variables. This method of partitioning variation has been widely used to model the spatial variation of species richness (e.g. Lobo & Martín-Piera, 2002; Ferrer-Castán & Vetaas, 2005). According to our results, it has also been proved appropriate for modelling the spatial variation of landscape composition and configuration.

Environmental variables have had a higher effect than geographical variables on landscape composition and configuration in Spain. Geographical factors were considered in models having controlled historical factors and therefore they enabled the segregation of purely environmental effects from geographical effects. Geographical Structured Environmental (GSE) fraction was small in most of landscape composition and configuration indices with the exception of forest plantation, *dehesa* and pastures land covers because their distribution is geographically restricted. *Dehesa*, mainly linked to cattle rearing, is widespread over oligotrophic soils. Thus, it should be expected to be the more envi-

ronmentally dependent landscape. Nevertheless, its restricted distribution overrides the detection of environmental dependence if it is analysed at the same scale than the other land uses. On the other hand, land uses such forest, *matorral* and crops show a wider distribution, which makes possible the evaluation of environmental dependence at a national scale. At least during the study period, forest and *matorral* have decreased their dependence on environment. At the same time, crop land cover type has increased its environmental dependence. This has been the consequence of crop abandonment in less productive areas such as stony slopes where forest plantations are currently found.

The influence of the climatic aridity gradient is higher than that of the lithology gradient for all land covers and the majority of configuration indices. Likewise, altitudinal variables are also significant. Similar results, highlighting the ability of the aridity gradient to explain land cover diversity, in contrast to lithology, have been observed at the regional scale in northern Spain (Nogués-Bravo, 2006).

However, there is still a high proportion of unexplained variation, which is most probably related to human actions that have not been included in the current analysis. The index that has had the highest proportion of unexplained variation is MSI, a complex shape index that has had no significant environmental effect, and only a low geographical effect (Table 4). This index is probably very much influenced by human decisions related to local land uses. Other environmental variables measured at inappropriate scales or not measured and

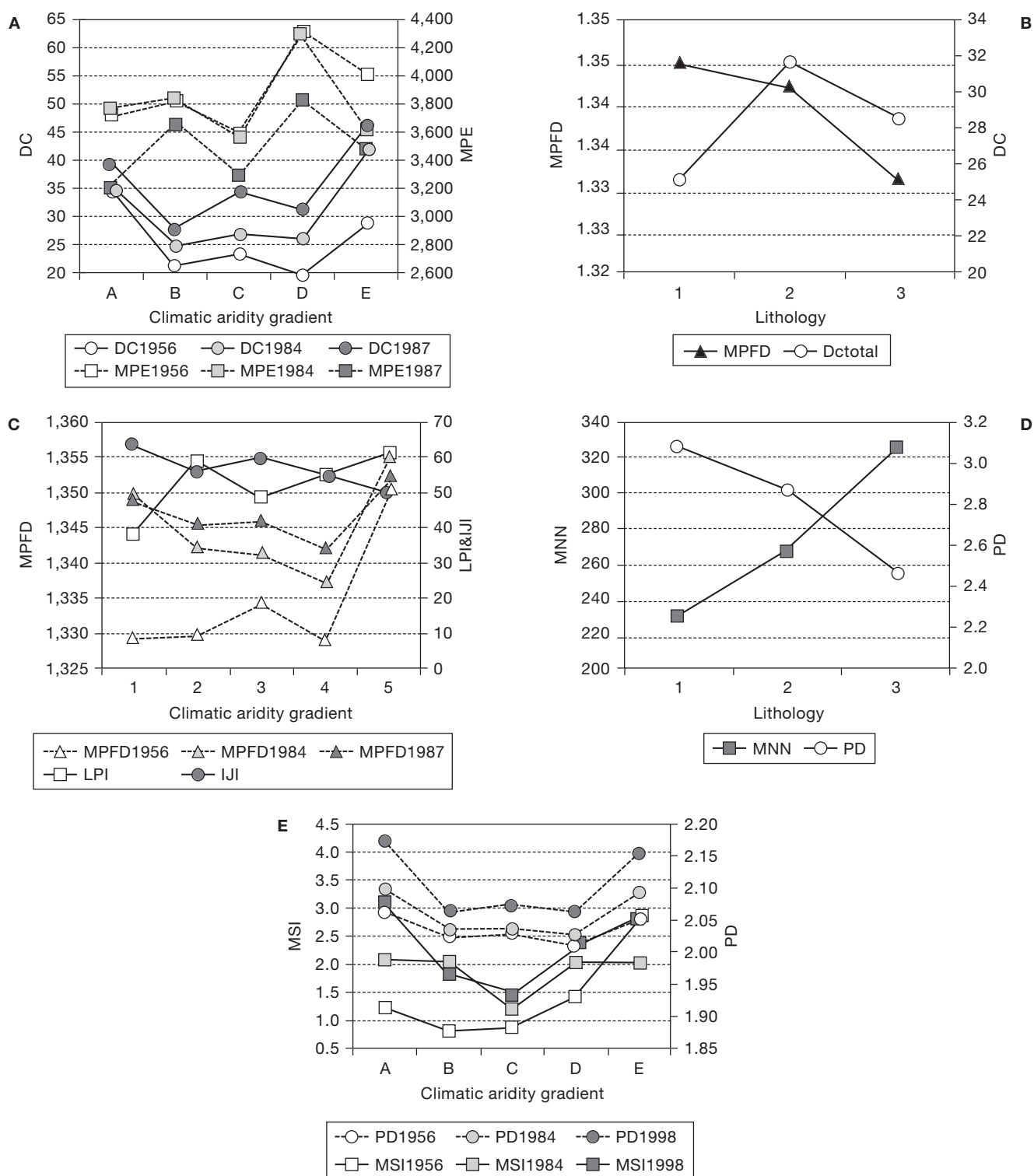


Figure 5. Relationships between landscape configuration indicators and two environmental gradients. A: Temporal variation of mean values of road network density (RD) and Mean Patch Edge (MPE) in relation with climatic aridity gradient. B: Mean values of Mean Patch Fractal Dimension (MPFD) and RD in relation to lithology. C: Mean values of Interspersion and Juxtaposition Index (IJI), Largest Patch Index (LPI) and temporal variation of MPFD in relation with climatic aridity gradient. D: Mean values of Mean Nearest Neighbour (MNN) and Patch Density (PD) in relation with lithology. E: Temporal variation of mean values of Mean Shape Index (MSI) and PD in relation with climatic aridity gradient. Ascendent sorted dates are indicated by increase of symbol size in (A), (C) and (E).

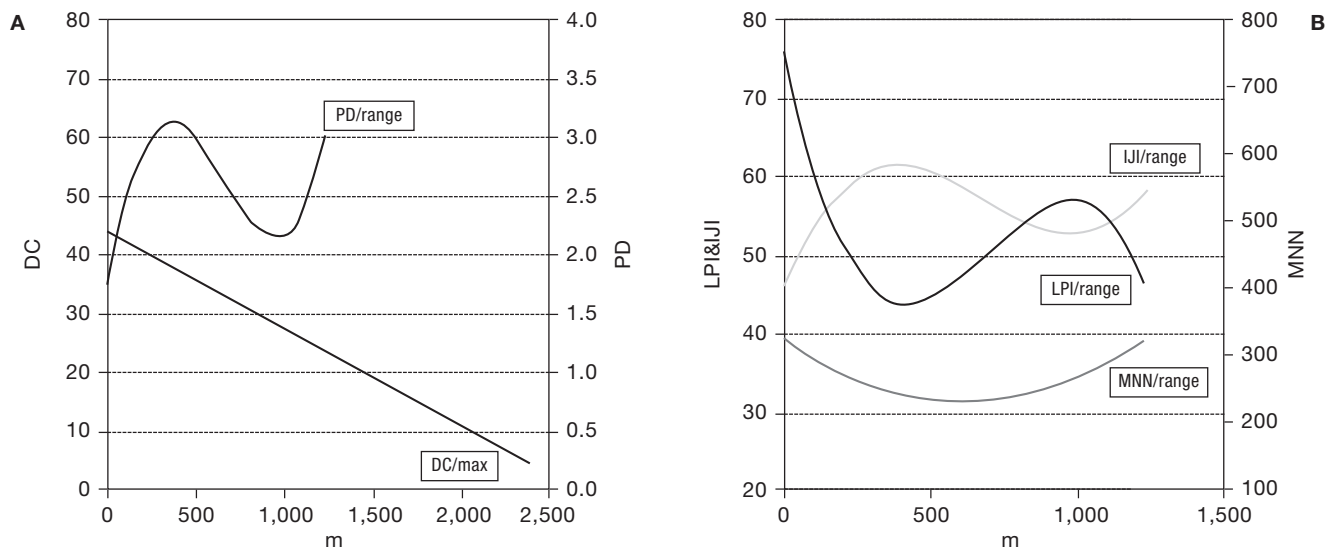


Figure 6. Figure 6. Relationships between landscape configuration indices and topography variables as a result of GLM fittings. A: Road network Density (RD) and Patch Density (PD) in relation with altitudinal Maximum and Range, respectively. B: Largest Patch Index (LPI), Interspersion and Juxtaposition Index (IJI) and Mean Nearest Neighbour (MNN) in relation to altitudinal Range.

noise in the data could also account for this lack of significance.

Environmental variables explained more variation in landscape composition than in configuration, suggesting that human action first influence configuration and then composition of landscapes. The existence of this relationship has generally been maintained over time, although it has been disturbed at local levels indicating few changes in landscape ecological pattern and hence in environmental dependence. Policies for the maintenance of landscape patterns therefore need to utilise an overall framework in order to determine which changes are detrimental to local character, as Álvarez-Cobelas *et al.* (2007) have recently suggested for degraded wetlands in semiarid areas of Spain.

Therefore, a global analysis of landscape pattern and its determinants in a country as Spain is a major tool to evaluate the environmental dependence of a region. Thus, landscape ecology has been used as holistic problem-solving oriented science, as proposed by Naveh (2000) and approached by Palang *et al.* (2000). The stability of the correlations means that, in policy terms, landscape change has not altered fundamental relationships during the study period. However, that is not to say that local character has remained unaltered. For example the coastal plain of Almería has been modified by the construction of plastic greenhouses to the extent that semi-natural habitats have almost disappeared. Policy makers therefore need to examine the inherent landscape ecological character of an area

Table 6. Correlations between landscape composition indicators and landscape configuration indices. Significant Pearson r at level less than 0.01 are indicated. The meaning of acronyms of landscape configuration indices is given in Table 2

Landscape composition indicators	Landscape configuration indices							
	PD	MPE	MSI	MPFD	MNN	IJI	LPI	RD
Forest	n.s.	n.s.	-0.11	-0.14	n.s.	0.12	n.s.	-0.22
Crops	n.s.	n.s.	0.19	0.34	n.s.	-0.31	0.35	0.32
<i>Dehesa</i>	-0.25	n.s.	-0.16	-0.28	0.29	n.s.	0.15	-0.14
<i>Matorral</i>	0.13	n.s.	n.s.	n.s.	-0.20	n.s.	-0.26	-0.26
Pastures	0.17	n.s.	-0.10	-0.14	n.s.	0.27	-0.24	n.s.
Forest Plantation	0.21	n.s.	n.s.	n.s.	n.s.	0.13	-0.28	0.16
Shannon Diversity Index	0.48	-0.10	n.s.	-0.13	-0.25	0.53	-0.86	n.s.
Patch richness	0.48	-0.41	n.s.	0.20	n.s.	0.13	-0.39	0.19

and determine policies to maintain that character. The recent initiative of the Spanish Government on limitation of development in coastal landscapes provides such an example, but the present results provide a framework for comparable policies to be developed in more complex rural landscapes.

Temporal changes of landscape composition and configuration

The areas of landscapes occupied by forest, *dehesa*, and pastures land uses types have not changed significantly between 1956 and 1998 (see Table 3). However, some of the configuration indices have changed over time although they are correlated with landscape composition indicators that have not changed, e.g.: forest is negatively correlated with MPFD, MSI and RD. Therefore, landscapes with a high proportion of forest and low road network density have probably changed because the landscape configuration has been altered by the increase of road network density, although the extent of forest area has not changed. This process of fragmentation has also occurred in *dehesa* and *matorral* landscapes, and it has been documented for other land cover types in Britain (see for instance, Haines-Young *et al.*, 2000).

In contrast, crop land cover type has decreased, and forest plantation has increased over the study period, but the configuration indices correlated to them remain unchanged. Landscape composition can therefore change over time without altering its spatial arrangement of patches. In fact different land covers have substituted the original ones, without changing the geometry of the patches.

On the other hand, landscape spatial configuration has changed over time independently of landscape composition because patches can change in composition but can also be spatially altered. Landscape indices that have increased are RD, PD, MSI and MPFD, and mostly reflect an increase in the fragmentation and the complexity of many landscapes. The increase of fragmentation due to expansion and intensification of human land use has been already recognised by Burgess & Sharpe (1981), and Jongman (2002). Both trends in landscape change demonstrate the relative independence of landscape composition and configuration and shows that they must therefore be analysed in separated models.

The methodology for assessing landscape change in Spain is based on the same principles used in other

countries of Europe e.g. the Countryside Survey 2000 of Great Britain (Haines-Young *et al.*, 2000). This system of monitoring is based on the statistical stratification procedure developed for regional survey by the Institute of Terrestrial Ecology and is designed to minimise personal judgement in sample site location (Bunce *et al.*, 1996a,b). The use of the Spanish rural landscape network SISPARES includes a comprehensive representation of rural landscapes throughout Spain according to the biogeoclimatic conditions (García del Barrio *et al.*, 2003). This landscape classification is also linked to other stratifications in Europe as described by Bunce *et al.* (2002) and its primary gradient is identical to that described in Metzger *et al.* (2005).

Conclusions

During the studied period, the effect of environmental variables on Spanish landscape composition and configuration has been more significant than that of geographical variables. Both composition and configuration were moderately correlated with environmental factors, but composition showed higher correlation levels than configuration.

In terms of dynamics, landscape composition in Spain has been relatively stable with few significant changes recorded between 1956 and 1998. On the contrary, landscape configuration has been changing, especially involving fragmentation processes.

Landscape composition was more dependent on environment than landscape configuration, probably because human decisions determine more the number, size and shape of patches than the changes of land cover type proportion in the landscape, at least in a short term period, as the one studied here.

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References

- ÁLVAREZ-COBELAS M., SÁNCHEZ-CARRILLO S., CIRUJANO S., ANGELER D.G., 2007. Long-term changes in spatial patterns of emergent vegetation in a Mediterranean floodplain: natural versus anthropogenic constraints. *Plant Ecology* 194(2), 257-271.
- BARR C.J., BUNCE R.G.H., CLARKE R.T., FULLER R.M., FURSE M.T., GILLESPIE M.K., GROOM G.H., HALLAM C.J., HORNUNG M., HOWARD D.C., NESS M.J., 1993. Countryside Survey 1990 Main Report, DoE, London.
- BOLAÑOS F.J., GARCÍA DEL BARRIO J.M., REGATO P., ELENA-ROSSELLÓ R., 2001. Spanish forested landscapes: classification and dynamics. In: *Development of European landscapes* (Mander Ü., Printsmann A., Palang H., eds). IALE European Conference. Volume 1. Institute of Geography, University of Tartu, Estonia. pp. 258-263.
- BORCARD D., LEGENDRE P., DRAPEAU P., 1992. Partialling out the spatial component of ecological variation. *Ecology* 73, 1045-1055.
- BUNCE R.G.H., CAREY P.D., ELENA-ROSELLÓ R., ORR J., WATKINS J., FULLER R., 2002. A comparison of different biogeographical classifications of Europe, Great Britain and Spain. *Journal of Environmental Management* 65, 121-134.
- BUNCE R.G.H., BARR C.J., CLARKE R.T., HOWARD D.C., LANE A.M.J., 1996a. Land classification for strategic ecological survey. *Journal of Environmental Management* 47, 37-60.
- BUNCE R.G.H., BARR C.J., CLARKE R.T., HOWARD D.C., LANE A.M.J., 1996b. The ITE meriewood land classification of Great Britain. *Journal of Biogeography* 23, 625-634.
- BURGESS R.L., SHARPE D.M., 1981. *Forest island dynamics in man-dominated landscapes*. New York, Springer-Verlag.
- DUNNING J.B., DANIELSON B.J., PULLIAM H.R., 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65, 169-175.
- EEA, 1995. CORINE land cover. Part II. Nomenclature. European Environmental Agency.
- EIDEN G., KAYADJANIAN M., VIDAL C., 2000. Quantifying landscape structures: spatial and temporal dimensions. In: *From land cover to landscape diversity in the European Union*. European Commission, Joint Research Center, Ispra.
- ELENA-ROSSELLÓ R., TELLA G., CASTEJÓN M., 1997. Clasificación biogeoclimática de España peninsular y balear. Ministerio de Agricultura pesca y Alimentación, Madrid, Spain.
- FERRER-CASTÁN D., VETAAS O.R., 2005. Pteridophyte richness, climate and topography in the Iberian Peninsula: comparing spatial and non-spatial models of richness patterns. *Global Ecology & Biogeography* 14, 155-165.
- FORMAN R.T.T., GODRON, M., 1986. *Landscape ecology*, John Wiley & Sons, New York.
- GARCÍA DEL BARRIO J.M., BOLAÑOS F., ELENA-ROSSELLÓ R., 2003. Landscape evolution in Spanish Atlantic mountains during the last five decades. In: *Landscape ecology and management of Atlantic mountains* (Pinto-Correia T., Bunce R.G.H., Howard D.C., eds) Proceedings of the joint APEP and IALE (UK) conference. Guarda, Portugal. pp. 103-111.
- HAINES-YOUNG R.H., BARR C.J., BLACK H.I.J., BRIGGS D.J., BUNCE R.G.H., CLARKE R.T., COOPER A., DAWSON F.H., FIRBANK L.G., FULLER R.M., FURSE M.T., GILLESPIE M.K., HILL R., HORNUNG M., HOWARD D.C., MC CANN T., MORECROFT M.D., PETIT S., SIER A.R.J., SMART S.M., SMITH G.M., STOTT A.P., STUART R.C., WATKINS J.W., 2000. Accounting for nature; assessing habitats in the UK countryside. DETR, London.
- HILL M.O., 1979. TWISPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University Press, Ithaca, New York.
- HONNAY O., PIESSENS K., VAN LANDUYT W., HERMY M., GULINCK H., 2003. Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. *Landscape and Urban Planning* 63, 241-250.
- JONGMAN R.H.G., 2002. Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape and Urban Planning* 58(2-4), 211-221.
- LEGENDRE P., 1990. Quantitative methods and biogeography analysis. *Evolutionary biogeography of the marine algae of the North Atlantic* (Garbary D.J., South R.R., eds). NATO ASI series. Springer-Verlag, Berlin. Vol G 22, pp. 9-34.
- LEGENDRE P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659-1673.
- LEGENDRE P., FORTIN M.J., 1989. Spatial pattern and ecological analysis. *Vegetatio* 80, 107-138.
- LEGENDRE P., LEGENDRE L., 1998. *Numerical ecology*. 2nd ed. Elsevier, Amsterdam.
- LOBO J.M., MATÍN-PIERA F., 2002. Searching for a predictive model for species richness of Iberian Dung beetle based on spatial and environmental variables. *Conservation Biology* 16(1), 158-173.
- MCGARIGAL K., MARKS B.J., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. USDA For Serv Gen Tech Rep PNW-351.
- MANDER Ü., JONGMAN R.H.G., 1998. Human impact on rural landscapes in central and northern Europe. *Landscape and Urban Planning* 41(3-4), 149-154.
- METZGER M.J., BUNCE R.G.H., JONGMAN R.H.G., MUCHER C.A., WATKINS J.W., 2005. A climatic stratification of the environment of Europe. *Global Ecology and Biogeography* 14(6), 549-563.
- NAVEH Z., 2000. What is holistic landscape ecology? A conceptual introduction. *Landscape and Urban planning* 50, 7-26.

- NOGUÉS-BRAVO D., 2006. Assessing the effect of environmental and anthropogenic factors on land-cover density in a Mediterranean mountain environment. *Area* 38(4), 432-444.
- PALANGH H., ALUMÈ H., MANDER U., 2000. Holistic aspect in landscape development: a scenario approach. *Landscape and Urban Planning* 50, 85-94.
- QUEZEL P., 1977. Los bosques de la cuenca mediterránea, en Bosque y Maquia mediterránea. Edit Serbal/Unesco, Barcelona.
- RIITTERS K.H., O NEILL R.V., HUNSAKER C.T., WICKHAM J.D., YAKEE D.H., TIMMINS S.P., JONES K.B., JACKSON B.L., 1995. A factor analysis of landscape pattern and structure metrics. *Landscape Ecol* 10(1), 23-39.
- SMITH R.S., 1982. The use of land classification in resource assessment and rural planning. Institute of Terrestrial Ecology, Natural Resource Environment Council.
- SNEDECOR G.W., COCHRAN W.G., 1980. *Statistical methods*. 7th ed. Iowa State University Press, Ames.
- STATISTICA for Windows, 1999. StatSoft, Inc. Computer program manual. StatSoft Inc, Tulsa.
- TER BRAAK C.J.F., 1987. *Canoco: a Fortram program for canonical community ordination*. Wageningen.
- TURNER M.G., GARDNER R.H., 1991. *Quantitative methods in landscape ecology*. Springer, New York.
- TURNER B.L., CLARK II W.C., KATES R.W., RICHARDS J.F., MATHEWS J.T., MEYER W.B., 1990. *The earth as transformed by human action. Global and regional changes in the biosphere over the past 300 Years*. Cambridge University Press, Cambridge.
- WHITTAKER R.J., WILLIS K.J., FIELD R., 2001. Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography* 28, 453-470.