RESEARCH PAPER

Identification of current ecosystem functional types in the Iberian Peninsula

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ABSTRACT

Aim To examine the geographical patterns of the interception of photosynthetically active radiation by vegetation and to describe its spatial heterogeneity through the definition of ecosystem functional types (EFTs) based on the annual dynamics of the Normalized Difference Vegetation Index (NDVI), a spectral index related to carbon gains.

Location The Iberian Peninsula.

Methods EFTs were derived from three attributes of the NDVI obtained from NOAA/AVHRR sensors: the annual integral (NDVI-I), as a surrogate of primary production, an integrative indicator of ecosystem functioning; and the intra-annual relative range (RREL) and month of maximum NDVI (MMAX), which represent key features of seasonality.

Results NDVI-I decreased south-eastwards. The highest values were observed in the Eurosiberian Region and in the highest Mediterranean ranges. Low values occurred in inner plains, river basins and in the southeast. The Eurosiberian Region and Mediterranean mountains presented the lowest RREL, while Eurosiberian peaks, river basins, inner-agricultural plains, wetlands and the southeastern part of Iberia presented the highest. Eurosiberian ecosystems showed a summer maximum of NDVI, as did high mountains, wetlands and irrigated areas in the Mediterranean Region. Mediterranean mountains had autumn–early-winter maxima, while semi-arid zones, river basins and continental plains had spring maxima. Based on the behaviour in the functional traits, 49 EFTs were defined.

Main conclusions The classification, based on only the NDVI dynamics, represents the spatial heterogeneity in ecosystem functioning by means of the interception of radiation by vegetation in the Iberian Peninsula. The patterns of the NDVI attributes may be used as a reference in evaluating the impacts of environmental changes. Iberia had a high spatial variability: except for biophysically impossible combinations (high NDVI-I and high seasonality), almost any pattern of seasonal dynamics of radiation interception was represented in the Peninsula. The approach used to define EFTs opens the possibility of monitoring and comparing ecosystem functioning through time.

Keywords

AVHRR/NOAA, classification, ecosystem functioning, land-use change, Normalized Difference Vegetation Index (NDVI), **regional analysis, remote sensing.**

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INTRODUCTION

Global change will drastically affect biodiversity through land-use and climate modifications (Vitousek *et al.*, 1997); the characterization of biodiversity elements as functional units allows for the assessment of the effects of these changes (Díaz & Cabido, 1997). In this sense, the most frequently used functional units have been plant functional types (PFTs). PFTs reduce the complexity of species diversity in ecological function to a few key plant types by grouping similarly functioning species independently of phylogeny (Noble & Gitay, 1996). Nevertheless, at any level of biological organization, elements that share a certain set of common structural or process features may be treated as a functional group. In fact, other studies have defined functional types at lower levels of

the biodiversity hierarchy (genes, molecules, etc.) and with other organism groups (Steneck, 2001). Several authors have pointed out the necessity of a functional classification of ecosystems (Körner, 1994; Valentini *et al.*, 1999; Paruelo *et al.*, 2001a). In this sense, as plant species can be grouped based on functional features (i.e. relative growth rates, nitrogen fixation) into PFTs, ecosystems can be grouped based on their functional behaviour into ecosystem functional types (hereafter EFTs). Also, as environmental transformations are particularly noticeable at the ecosystem level (Vitousek *et al.*, 1997), knowledge of the temporal and spatial patterns of ecosystem functioning at the regional scale provides a proper background to assess the effects of environmental changes (Gitay & Noble, 1997).

Mueller-Dombois and Ellenberg (1974) pointed out that vegetation classification could be based on interdependencies in the functional sense between vegetation and the environment, emphasizing in this way functional similarities between different ecosystems. Considering functional variables in the definition of ecosystems clearly complements and improves the descriptions based on only structural features (Valentini *et al.*, 1999) and shows some advantages: (1) functional classifications provide a useful framework to understand large-scale ecological changes in relation to ecosystem function and processes; (2) the inertia of structural attributes may delay the perception of ecosystem responses to environmental changes, while the exchange of energy and matter of an ecosystem has a shorter response (Milchunas & Lauenroth, 1995); (3) monitoring of functional attributes with satellite imagery is easier than for structural ones (Paruelo *et al.*, 2001a); and (4) functional attributes allow the qualitative and quantitative assessment of ecosystem services (Costanza *et al.*, 1997).

Different approaches have been proposed for the definition of functional units at the ecosystem level, using both top-down and bottom-up strategies. Shugart (1997) was one of the first to use the term EFT as 'aggregated components of ecosystems whose interactions with one another and with the environment produce differences in patterns of ecosystem structure and dynamics' (i.e. the way in which plants modify ecosystem dynamics in the sense of functional effect types of Díaz & Cabido, 2001). Walker (1997) proposed the use of a similar term, vegetation functional types, for groups of PFTs in sets that constitute the different states of vegetation succession in non-equilibrium ecosystems. The same term was applied by Scholes *et al.* (1997) in a wider sense for those areas having similar ecological attributes, such as PFTs composition, structure, phenology, biomass or productivity. Several studies have applied hierarchy and patch dynamic theories (Aber *et al.*, 1999; Reynolds & Wu, 1999; Wu *et al.*, 2003) for the definition of ecosystem and landscape functional types at different spatial scales, by scaling-up emergent structural and functional properties from patches to region. Valentini *et al.* (1999) defined functional units by focusing on patches of the land surface that are able to exchange mass and energy with the atmosphere and show a coordinated and specific response to environmental factors. They also made an attempt to aggregate functional properties in order to achieve a functional classification of ecosystems, with a specific focus on processes involved in

biosphere–atmosphere exchanges. These ideas have been developed in several works (e.g. Falge *et al.*, 2002) that assessed the applicability of FLUXNET data to evaluate EFTs in terms of their differences in net ecosystem CO_2 exchange, which is crucial for scaling-up flux estimates on eddy-covariance towers to landscape and global scales.

Remote sensing techniques provide valuable tools to classify ecosystems at the regional scale (e.g. Lloyd, 1990; Nemani & Running, 1997). Mueller-Dombois and Ellenberg (1974) suggested the use of solar energy by green plants as a parameter worthy for a functional quantitative characterization of ecosystems. Hence, functional traits derived from satellite data and related to carbon and water cycles are suitable variables to define EFTs. This is the case of the approach by Paruelo *et al.* (2001a) for temperate South America. EFTs were defined separately from vegetation structure as a group of ecosystems sharing functional characteristics that included the amount and timing of matter and energy exchanged between the biotic community and the environment (in the same sense as Valentini *et al.*, 1999). The functional variables they used in their classification focused on the dynamics of primary production, one of the essential and most integrative indicators of ecosystem functioning (McNaughton *et al.*, 1989; Virginia & Wall, 2001). For this purpose, they used three attributes of the seasonal dynamics of the Normalized Difference Vegetation Index (NDVI). This is an spectral index closely related to above-ground net primary productivity (ANPP) (Tucker & Sellers, 1986; Sellers *et al.*, 1992) and a linear estimator of the fraction of absorbed photosynthetically active radiation (fAPAR) by vegetation (Sellers *et al.*, 1996; Fensholt *et al.*, 2004; Wang *et al.*, 2004).

Here, we used the Iberian Peninsula (Fig. 1) as a suitable region to test and implement a classification based on functional attributes of ecosystems. As previous studies have remarked (Lloyd, 1989; Lobo *et al.*, 1997), Iberia has many desirable properties for remote sensing studies. Despite its size (581,000 km²), it has remarkable landscape diversity as a consequence of its relief, climate, geological features and biogeographical location (transition between the Eurosiberian and Mediterranean Regions according to Rivas-Martínez, 1987). Nowadays, a large part of Iberia has a relatively low human population and croplands have decreased considerably in the last few decades. There is a wide knowledge of the Iberian ecosystems in terms of its vegetation structure and floristic composition (e.g. Rivas-Martínez, 1987; Costa *et al.*, 1998), and important structural (Peñuelas & Boada, 2003) and functional (Vicente-Serrano & Heredia-Laclaustra, 2004) changes have been documented due to climate modifications. Remote sensing studies based on NDVI have been used largely under a wide range of environmental conditions in Iberia to estimate biomass, leaf area index, vegetation stress, fAPAR and productivity (e.g. Calvao & Palmeirim, 2004; Filella *et al.*, 2004).

Currently, the Iberian Peninsula is proving to be a lively research area in relation to global change and ecosystem functioning (e.g. Shoshany, 2000; Arribas *et al.*, 2003; González-Alonso *et al.*, 2004; Peñuelas *et al.*, 2004). Some of these works were based on NOAA/AVHRR NDVI temporal series. Lloyd
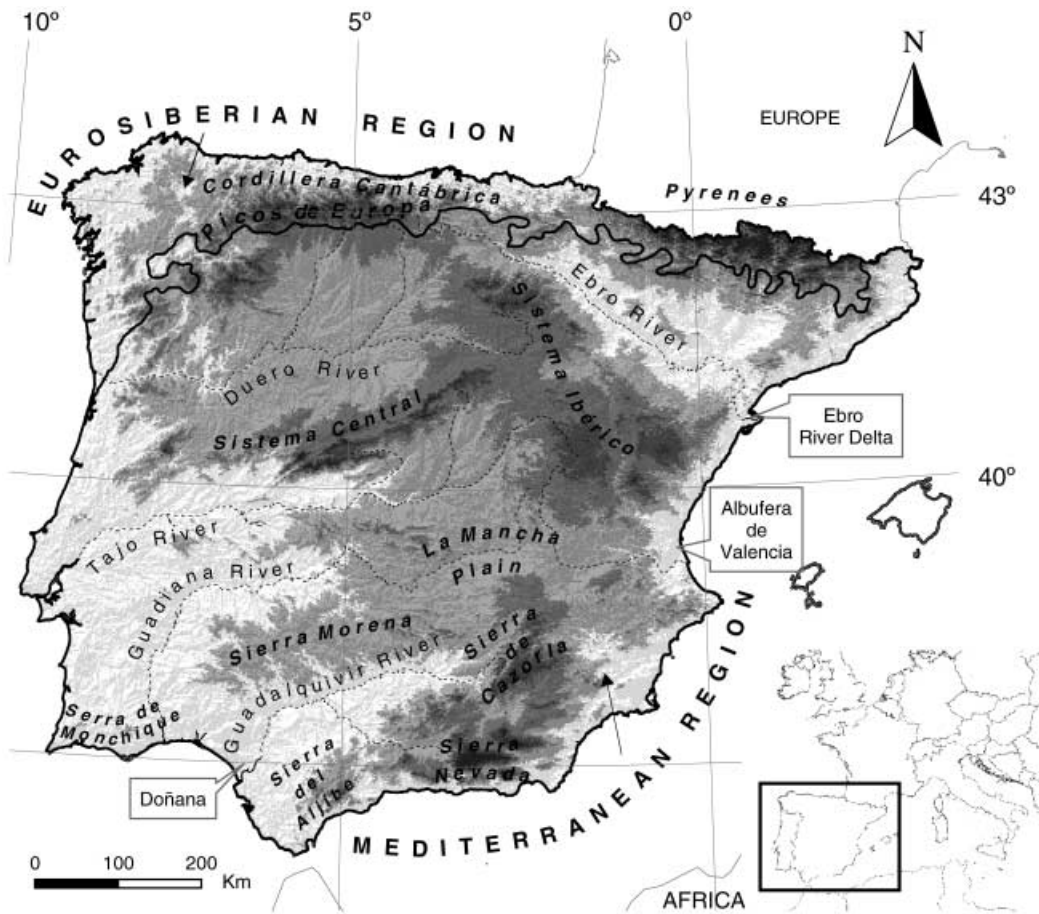
Figure 1 Study area. Biogeographical regions and main geographical features of the Iberian Peninsula mentioned in the text.

(1989) carried out a multitemporal characterization of different Iberian vegetation structures with 2 years (1985–86) of images from April to October. Lobo *et al.* (1997) explored the power of NDVI temporal series (1984–88) to resolve vegetation types using hierarchical classification methods. Azzali and Menenti (1999) constructed maps of vegetation units characterized by homogeneous foliar phenology (isogrowth zones) by using Fourier analysis with 10-day composites of maximum NDVI for 1995.

Following the rationale of Paruelo *et al.* (2001a), in this article we describe the functional diversity of the Iberian Peninsula at the regional scale by defining EFTs from the dynamics of carbon gains using traits derived from the seasonal dynamics of the NDVI for the period 1982–99. Our specific objectives were:

1 to describe the main patterns of the interception of radiation by vegetation from three attributes of the NDVI annual curve (the annual integral, the interseasonal variability and the date of maximum NDVI);

2 to define, based on such traits, EFTs for the Iberian Peninsula; and

3 to analyse the correspondence between the functional units defined and potential vegetation and land-use types, and to get the main controls of the spatial distribution of EFTs in the Iberian Peninsula.

METHODS

We based our analysis on mean monthly NDVI values for the period 1982–99. The NDVI is a spectral index calculated from the reflectance in the red (channel 1, 580–680 nm) and near infrared (channel 2, 725–1100 nm) bands as follows (Tucker & Sellers, 1986): $NDVI = (NIR - R)/(NIR + R)$. Our data set consisted of 10-day NDVI composites provided by the Global Land Cover 8 km AVHRR Project (Pathfinder AVHRR Land–PAL data set). This data base comes from NOAA-7, -9 and -11 satellite imageries and was radiometrically and spatially corrected (for details see James & Kalluri, 1994). The scenes have an approximate spatial resolution of 8×8 km and cover the whole globe. We used the portion of the images located between 35° N and 45° N latitude and 3.5° E and 10.2° W longitude in correspondence with the Iberian Peninsula. The period considered (1982–99) includes both extremely dry and wet periods for the Peninsula (Arribas *et al.*, 2003; Sumner *et al.*, 2003).

Once the composites were imported to ERDAS Imagine 8.4, they were layer-stacked to create a 36-band image for each year. To minimize noise and spurious values not removed by the original processing of the PAL data base, negative and extreme values were eliminated. Those problems associated with cloud

contamination, off-nadir views and sensor degradation were also minimized by selecting the maximum NDVI value for each pixel from the three 10-day composites of each month. The monthly NDVI images were examined visually to check for further possible erroneous pixels to be removed manually. The final range of NDVI values varied between 0 and 0.8.

To describe the patterns of the interception of radiation by vegetation, the following variables were derived from the seasonal NDVI curve of the averaged year (Appendix S1 in Supplementary Material): annual integral (NDVI-I); annual relative range (RREL) (difference between maximum and minimum NDVI divided by annual integral); and month of the absolute maximum of NDVI (MMAX). These three variables describe in a conceivable way the height and shape of the annual NDVI curve and have biological significance (Pettorelli *et al.*, 2005). They have been reported to capture important features of ecosystem functioning for temperate ecosystems (Lloyd, 1990; Paruelo & Lauenroth, 1995; Nemani & Running, 1997; Paruelo *et al.*, 2001b). NDVI-I has been used as an integrative indicator of ecosystem functioning as it is a linear estimator of fAPAR (Sellers *et al.*, 1996) and thus of ANPP (Tucker & Sellers, 1986; Sellers *et al.*, 1992; Paruelo *et al.*, 1997). It has been employed from cool, moist temperate rain forests to Mediterranean forests and shrublands and even in hot deserts (e.g. Lloyd, 1990; Ricotta *et al.*, 1999; Stoms & Hargrove, 2000; Hoare & Frost, 2004). RREL provides a description of the intra-annual variation of photosynthetic activity, which has been used as an indicator of the seasonality of carbon fluxes (Oesterheld *et al.*, 1998; Potter & Brooks, 1998; Guerschman *et al.*, 2003). MMAX is a good descriptor of vegetation phenology, indicating the intra-annual distribution of the period with maximum photosynthetic activity (Lloyd, 1990; Hoare & Frost, 2004).

We examined the meaningfulness of these three attributes for describing the NDVI annual curve in the Iberian Peninsula. A principal component analysis (PCA) was carried out using the 12 NDVI values of the annual curve for the whole Peninsula and for the Eurosiberian and Mediterranean Regions separately. We then analysed the correlation between the functional attributes (NDVI-I, RREL and MMAX) and the first two principal axes of each PCA separately. We also tested correlation among the three variables.

The functional classification was carried out by identifying subsets of the three-dimensional space defined by the functional variables NDVI-I, RREL and MMAX. For this, we avoided classifications based on automatic clustering algorithms because they are data-dependent and did not keep the spatial patterns that could be recognized in the RGB false-colour image of the three traits that were clearly related to geographical and bioclimatic features. Instead we used a 'fixed' classification method to maximize the biological meaning and interpretability of the classes. Also, such an approach will allow the use of the same classification rules in further analysis on an annual basis, and provides a way to achieve a simple functional classification that produces ecologically interpretable outputs. Following the logic of Noble and Gitay (1996) in developing functional classifications we decided to start from the most simple, as long as outputs were ecologically interpretable. Four intervals of each attribute

Table 1 Range of the functional traits used in the definition of ecosystem functional types (EFTs) of the Iberian Peninsula: NDVI integral (NDVI-I), relative range of NDVI (RREL) and month of the maximum NDVI (MMAX). Capital letters correspond to the NDVI-I level, ranging from *A* to *D* for low to high NDVI-I. Small letters show the relative range, ranging similarly from *a* to *d* for low to high RREL. The numbers indicate the season of maximum NDVI

	Functional code	Lower limit	Upper limit
NDVI-I	A	0.099	0.250
	B	0.250	0.400
	C	0.400	0.550
	D	0.550	0.680
RREL	a	0.070	0.290
	b	0.290	0.515
	c	0.515	0.920
	d	0.920	2.254
MMAX	1	Summer	
	2	Autumn and early winter	
	3	Late winter and early spring	
	4	Late spring	

(Table 1) produced a relatively low number of potential classes ($4 \times 4 \times 4 = 64$) and allowed for the maintenance in the final classification of the patterns observed for the variables in the RGB image. We looked for the three highest spatial discontinuities in the NDVI-I and RREL maps. In order to obtain four intervals, the way we proceeded was based on selecting those three values where a relatively abrupt fall or increase in the spatial profile of the variable occurred. For MMAX, we also grouped the 12-month image into only four classes, which were in close correspondence with the four seasons that occur in temperate ecosystems. In this case, to keep the continuous nature of the annual period and the relative distance between months (i.e. December is as close to January as July is to June), we transformed months into polar coordinates. The entire circumference of a year was divided into 12 portions and each month was equated to an angle (30° for January and 360° for December). Months were therefore characterized by its sine and cosine values. All pixels of this two-band image were classified into four clusters using the ISODATA method (Iterative Self Organizing Data Analysis) that corresponded to the four seasons of the year in temperate ecosystems. The use of this synthetic variable increased the spatial continuity of the functional classification and made the interpretation of the phenological spatial patterns easier.

Each class was named as an EFT following the terminology suggested by Paruelo *et al.* (2001a). We assigned codes to each EFT based on two letters and a number (three characters) related to the interval value of each trait used in the definition of the classes (NDVI-I, RREL and MMAX). The first letter of the code (capital) corresponded to the NDVI-I level, ranging from *A* to *D* for low to high NDVI-I. The second letter (small) showed the relative range, ranging similarly from *a* to *d* for low to high RREL. The numbers indicated the season of maximum NDVI (see Table 1). The definition and coding of EFTs were based only on

functional attributes and allow for an ecological interpretation of the legend.

According to the correspondence among EFTs, potential vegetation and land-cover units, we identified the main controls of the spatial patterns of the EFTs. We evaluated the correspondence between the current functional units and potential vegetation through a correspondence analysis (CA) of the contingency matrix resulting from cross-tabulating the EFTs with a digital map compiled from vegetation series maps (Rivas-Martínez, 1987; Rivas-Martínez *et al.*, 1990; Costa *et al.*, 1998; Valle *et al.*, 2003). We grouped original vegetation series into 11 main potential vegetation types: Mediterranean evergreen oak forests; semi-deciduous forests; broad-leaved deciduous and mixed forests; birch forests; Eurosiberian coniferous forests; beech forests; *Juniperus thurifera* L. arborescent matorral; Mediterranean maquis; Iberian–African arborescent scrub and arid garrigues; oro-Mediterranean grasslands and scrubs; and wetlands and hydrophytic vegetation (see Appendix S2 in Supplementary Material). We also carried out a CA between EFTs and current land-cover types based on PELCOM (Pan-European Land Cover Monitoring Project: http://cgi.girs.wageningen-ur.nl/cgi/projects/eu/pelcom/) with 1×1 km of spatial resolution. To make a more comprehensive ordination analysis, both CAs were performed including EFTs that covered up to 90% of the Iberian surface. The assessment of the correspondence between our classes and the potential vegetation and land-cover maps were not intended to be an evaluation of our approach but an objective assessment of the agreement between structural and functional descriptions of current ecosystems at the regional level in a very human modified area such as the Iberian Peninsula.

RESULTS

The PCA axes were very similar for the whole Peninsula and for the Mediterranean Region (Table 2). The scores of the first axis of the PCA were all positive and similar. The first axis was basically the same as the average NDVI. Not surprisingly, for both the whole data set and the Mediterranean and Eurosiberian Regions, NDVI-I was strongly correlated with the first axis of the PCA

($r = 0.999$, $n = 9361$, $P < 0.001$; $r = 0.999$, $n = 8221$, $P < 0.001$ and $r = 0.998$, $n = 1140$, $P < 0.001$; respectively). The scores of the second axis were a contrast between the NDVI during summer months (showing negative values) and winter months (displaying positive values) and can be perceived as the contrast between minimum and maximum NDVI values. The correlation between RREL and the absolute value of the second axis was higher for the Eurosiberian Region ($r = 0.865$, $n = 1140$, $P < 0.001$) than for the whole data set ($r = 0.614$, $n = 9361$, $P < 0.001$) and the Mediterranean Region ($r = 0.585$, $n = 8221$, $P < 0.001$). The correlation between the NDVI-I and RREL was -0.568, despite the relationship that both had with the first two axes of the PCA (orthogonal by definition). The third variable included (MMAX) showed a low correlation with both NDVI-I and RREL (0.17 and -0.33, respectively). RREL also showed a high correlation coefficient ($r = 0.99$, $n = 9361$, $P < 0.01$) with coefficient of variation of the NDVI seasonal curve (CV = standard deviation divided by mean). This last statistic has also been employed as an estimator of the variability of the bioclimatic controls of ecosystem dynamics in the Iberian Peninsula (Montero de Burgos & González-Rebollar, 1983).

The three attributes of the NDVI curves for the averaged year showed a clear and contrasting pattern across Iberia. The Peninsula covered a high spatial variability in NDVI-I, ranging from 0.1 to almost 0.7 (Fig. 2a). The highest values were reached in the Eurosiberian Region and in the highest altitudes of the Mediterranean ranges. Low values occurred in the basins associated with major rivers, such as Ebro in the east or Duero in the north and in La Mancha inner plain. The semi-arid zones of southeastern Iberia showed the lowest values.

The Peninsula was highly variable in terms of seasonality. RREL (Fig. 2b) was high in the peaks of the Eurosiberian ranges (Pyrenees and Picos de Europa). River basins, inner plains (extremely modified by agriculture), rice fields and wetlands (Doñana, Ebro River Delta and Albufera de Valencia), and the semi-arid southeastern portion of Iberia showed the highest values for the Mediterranean Region. In general, RREL was low for the Eurosiberian Region and for the Mediterranean mountains.

Table 2 Eigenvectors and cumulative variance accounted for by the first two components of a principal component analysis (PCA) performed on the mean monthly NDVI values for the period 1982–99. Scores and explained variance of first and second axes differed between the whole Iberian Peninsula and the two biogeographical regions (Eurosiberian and Mediterranean)

|	Axis	Cumulated Variance	Scores											
			JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
Iberian	1	81%	0.898	0.864	0.840	0.846	0.907	0.913	0.904	0.899	0.908	0.952	0.961	0.922
Peninsula (IP)	2	93%	−0.355	−0.478	−0.496	−0.355	0.047	0.334	0.407	0.411	0.396	0.250	−0.020	−0.234
Mediterranean	1	75%	0.900	0.866	0.803	0.773	0.810	0.829	0.865	0.856	0.876	0.935	0.940	0.901
Region of IP	2	89%	−0.333	−0.462	−0.543	−0.435	−0.014	0.407	0.468	0.465	0.446	0.243	−0.062	−0.241
Eurosiberian	1	66%	0.843	0.864	0.858	0.885	0.912	0.729	0.603	0.628	0.693	0.902	0.919	0.860
Region of IP	2	92%	−0.498	−0.473	−0.487	−0.399	0.055	0.600	0.763	0.743	0.670	0.318	−0.220	−0.424
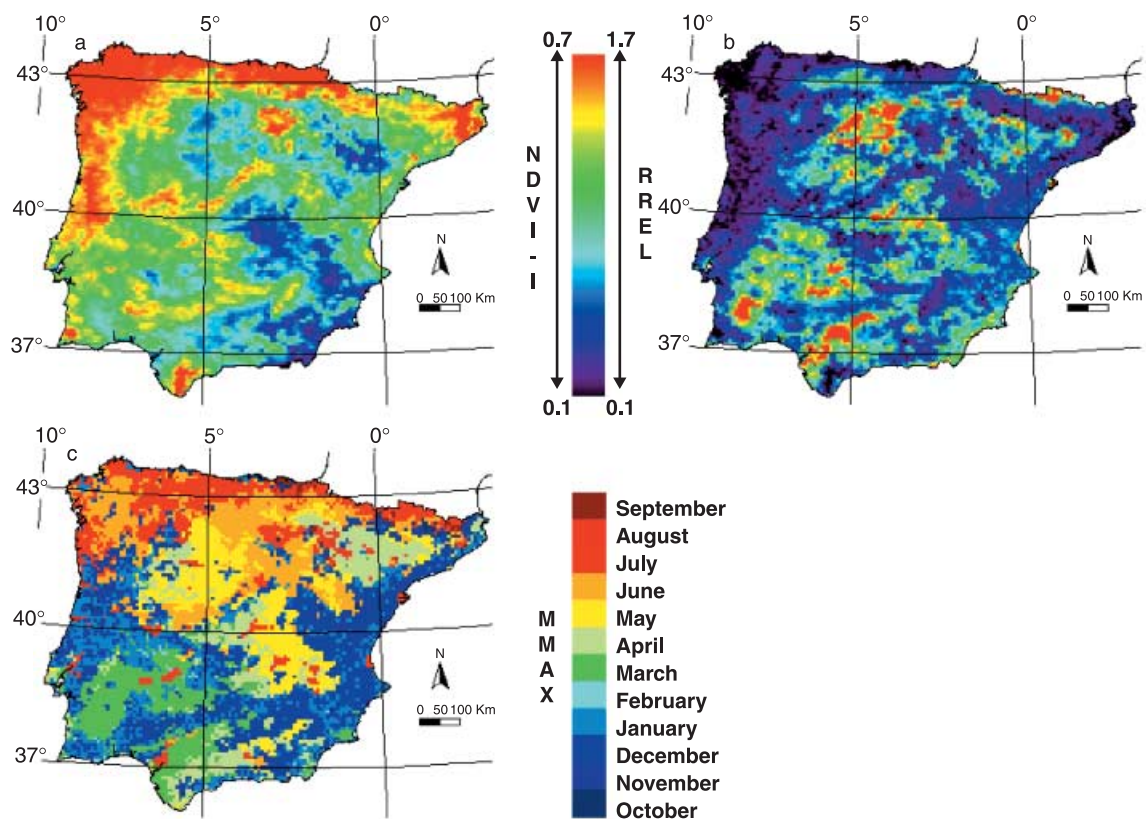
Figure 2 Patterns of the Normalized Difference Vegetation Index (NDVI) attributes across the Iberian Peninsula: (a) NDVI Annual integral (NDVI-I), (b) annual relative range of NDVI (RREL), and (c) month of the maximum NDVI (MMAX).

The Eurosiberian ecosystems were characterized by a clear summer NDVI maximum (Fig. 2c). In the Mediterranean Region, high mountains, wetlands and watered areas (riverine areas or irrigated crops) also showed their maximum in summer. The rest of the Peninsula had two main phenological patterns. Mediterranean mountains peaked in autumn–early winter, while semi-arid zones, river basins and continental plains had a spring maximum.

Twenty-two of the 64 possible EFTs occupied 90% of the Peninsula surface (Fig. 3). Classes *Ca2* and *Cb2* (that differed only in their seasonality) occupied 22% of the Iberian territory. Both corresponded mainly to Mediterranean evergreen oak forests, the most abundant potential vegetation unit of the Peninsula (Appendix S2). Fifteen of the 64 possible EFTs were not represented (0 pixels) or occupied very small areas (less than 10 pixels) (Fig. 4). In such a way, no EFT had at the same time extremely high values of NDVI-I and RREL (*Dd*). Only in the northern mountainside of the Pyrenees and Picos de Europa (Eurosiberian region) did some pixels show very high values of NDVI-I and high values of RREL (*Dc1*). At the other extreme, combinations of very low values of both NDVI-I and RREL at the same time were very rare (*Aa*). Other EFTs without representation were *Ac1*, *Ad1*, *Cd2*, *Cd3*, *Db2*, *Db4*, *Dc2*, *Dc3* and *Dc4* (Fig. 4).

EFTs with very high values of NDVI-I (*D*) were only observed in areas with low RREL (*a* and *b*). In general, they showed summer maximum and were distributed in the Eurosiberian Region and in the tallest Mediterranean mountains (*Da1*

and *Db1* occupied 11% of the Iberian surface). The rest of the *D* EFTs, mostly with autumn and early winter maxima (*Da2*), occurred mainly in the Mediterranean–Eurosiberian mountainous transition (subAtlantic and subMediterranean vegetation). Some areas of the southwest, in the Mediterranean Region (such as Sierra del Aljibe, western Sierra Morena and Serra de Monchique; see Fig. 1), also corresponded to this NDVI-I class (*Da2*). EFTs with very low values of NDVI-I (*A*) were relatively scarce and occurred in semiarid areas of the La Mancha plains, Ebro river basin and the south-eastern portion of the Iberian Peninsula. Only endorheic basins of the La Mancha plains (*Ab1*) showed extremely low NDVI-I-values with summer maxima. EFTs with very high values of RREL (*d*) were associated mainly with low values of NDVI-I (*B*) and with maxima from late winter to late spring (*3* and *4*). Only the highest parts of the Pyrenees, with a maximum in summer, had very high values of RREL and relatively high values of NDVI-I (*Cd1*). Fourteen pixels on the shores of the major rivers showed the same pattern but with an earlier maximum in spring (*Cd4*). Very low values of RREL (*a*) were associated with high and very high NDVI-I-values and with summer and autumn and early winter maxima (*1* and *2*).

Those EFTs with a summer maximum (30% of the Peninsula) tended to show high productivity and low seasonality (Fig. 4). On the contrary, ecosystems with winter and early spring maxima (17% of the Peninsula) tended to show low and medium productivity
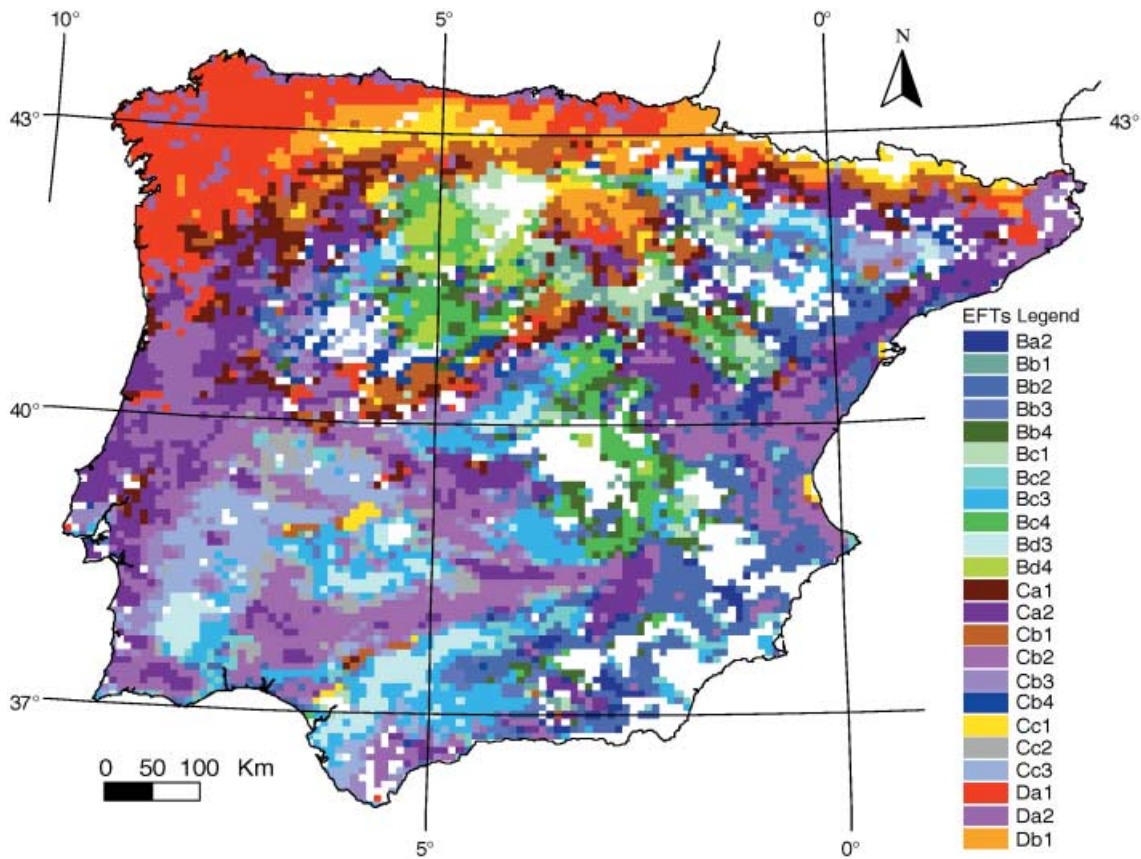
Figure 3 Ecosystem functional types (EFTs) for the Iberian Peninsula based on the NDVI dynamics. Only EFTs up to 90% of the Peninsula surface are shown.

and low to very high seasonality. A small proportion of ecosystems had their maximum in spring (11% of the Peninsula) and tended to have low values of NDVI-I and low to medium RREL. Autumn and early winter maxima occurred in 42% of the territory and had low RREL values and moderate to high productivity.

The first axis (dimension 1) of the CA ordination between potential vegetation and EFTs accounted for 50.32% of total variation in the data. Productivity and bioclimate formed gradients along dimension 1 (Fig. 5). Potential vegetation that scored low (Iberian–African arborescent scrubs and arid garrigues, Mediterranean maquis) was associated with low NDVI-I and Mediterranean and arid conditions, while potential vegetation with high scores (broad-leaved deciduous and mixed forests, beech forests, birch forests) was associated with high NDVI-I and more humid conditions of the Eurosiberian Region. The second axis (dimension 2) explained 24.29% of the variation. Seasonality formed a gradient along dimension 2. This last gradient was discernible only for high productive vegetation classes. Vegetation with low RREL had low scores on dimension 2 (broad-leaved deciduous and mixed forests) while those correlated with medium and high RREL scored high (beech forests, birch forests, Eurosiberian coniferous forests). Based on χ^2 distances and the CA scatterplot (Fig. 5, Appendix S3a in Supplementary Material), a partial correspondence between some EFTs and potential vegetation types was found. *Da1* ($\chi^2 = 2582$) and *Da2* ($\chi^2 = 287$) were associated with broad-leaved deciduous and mixed forests; *Db1* ($\chi^2 = 1132$)

with beech forests; *Cc1* ($\chi^2 = 379$) with Eurosiberian coniferous forests; and *Ca1* ($\chi^2 = 334$) with semideciduous forests.

In the CA ordination between land-covers and EFTs, the first axis (dimension 1) accounted for 58.37% of the total variation in the data, and was related to a productivity gradient. Land-covers with low scores (rainfed arable lands) were associated with low NDVI-I, while land-covers with high scores (forests) were associated with high NDVI-I. No discernible gradients along the second axis (dimension 2) were present. The CA scatterplot and the χ^2 distances between data points revealed the following narrow correspondences between some EFTs and particular land-uses (Fig. 6, Appendix S3b in Supplementary Material): *Bc4* ($\chi^2 = 173$) and *Bd3* ($\chi^2 = 230$) were associated with rainfed arable land; *Bc2* ($\chi^2 = 49$) with permanent crops; and *Bb2* with permanent crops ($\chi^2 = 213$) and barren land ($\chi^2 = 324$). As in the CA between EFTs and potential vegetation, *Da1* ($\chi^2 = 247$), *Da2* ($\chi^2 = 270$) and *Db1* ($\chi^2 = 158$) were related to forest land-cover.

DISCUSSION

Patterns of the NDVI traits in the Iberian Peninsula

As in other temperate areas (Townshend *et al.*, 1985; Paruelo & Lauenroth, 1995) the annual integral of NDVI, a surrogate of ANPP that was correlated strongly with the first PCA axis in our data set, accounted for most of the total variance in the annual dynamics
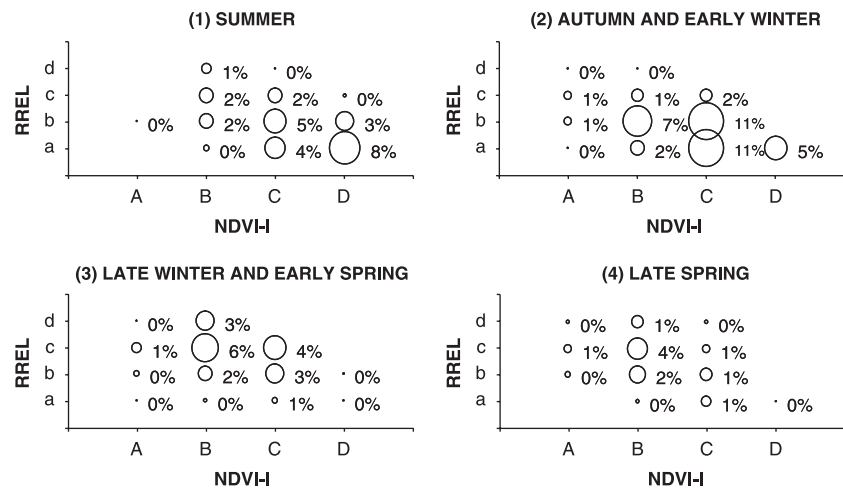
Figure 4 Frequency distributions of the ecosystem functional types (EFTs) in the Iberian Peninsula established upon a simple three-dimensional histogram partition based on three Normalized Difference Vegetation Index (NDVI) attributes: NDVI integral (NDVI-I), relative range of NDVI (RREL) and month of the maximum NDVI (MMAX).
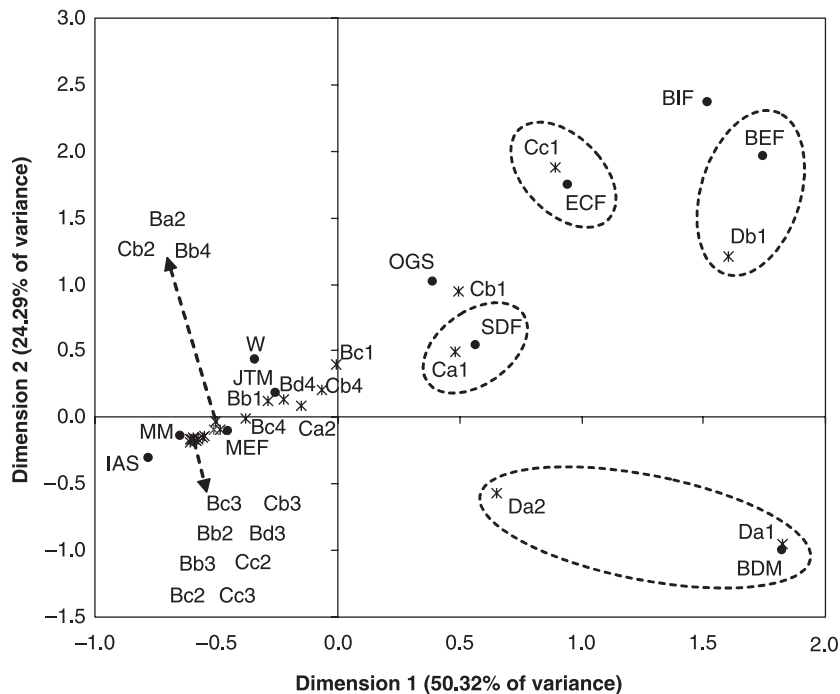

Figure 5 Ordination plot of dimension 1 and dimension 2 of the correspondence analysis (CA) run with the contingency matrix between potential vegetation units (circles) and ecosystem functional types (EFTs; asterisks) in the Iberian Peninsula. Only EFTs up to 90% of the Iberian surface were used. Significant associations were circled based on χ² distances (Appendix S3a). BDM = broad-leaved deciduous and mixed forests; BIF = birch forests; ECF = Eurosiberian coniferous forests; BEF = beech forests; SDF = semideciduous forests; JTM = *Juniperus thurifera* L. arborescent matorral; MEF = Mediterranean evergreen oak forests; MM = Mediterranean maquis; IAS = Iberian–African arborescent scrub and arid garrigues; OGS = Oro-Mediterranean grasslands and scrubs; and W = wetlands and hydrophytic vegetation. For codes of EFTs see Table 1: capital letters correspond to the NDVI-I level, ranging from *A* to *D* for low to high NDVI-I. Small letters show the relative range, similarly ranging from *a* to *d* for low to high RREL. The numbers indicate the season of maximum NDVI.

of the NDVI over the Iberian Peninsula (Table 2). This occurred even when we considered both biogeographical regions separately (Mediterranean and Eurosiberian). As a general pattern, NDVI-I decreased gradually southwards and eastwards. The second axis of variation, where we perceived a strong contrast between the scores for the summer and winter months, was related to phenology and had differential importance in the two biogeographical

regions. The weight of the difference between maximum and minimum values of NDVI (RREL in our analysis) in capturing the variance of the NDVI dynamics was relatively more important in the Eurosiberian Region than in the Mediterranean Iberia (Table 2). Although phenology is a fundamental source of variation for the Iberian Peninsula, as found in previous studies (Lobo *et al.*, 1997) based on a 5-year data set of NOAA/AVHRR images, results
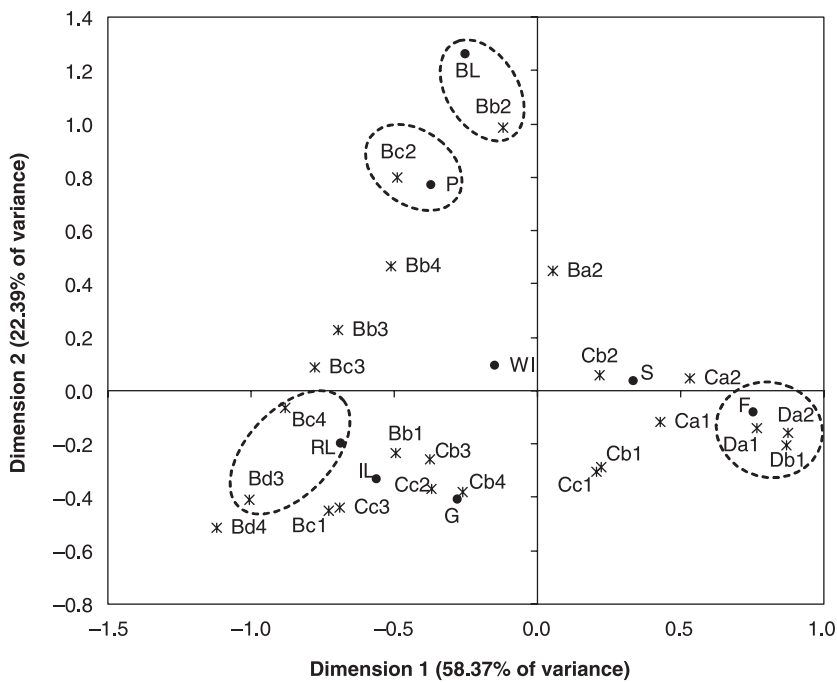
Figure 6 Ordination plot of dimension 1 and dimension 2 of the correspondence analysis (CA) run with the contingency matrix between land-covers (circles) and ecosystem functional types (EFTs; asterisks) in the Iberian Peninsula. Only EFTs up to 90% of the Iberian surface were used. Significant associations were circled based on χ^2 distances (Appendix S3b). F = forests, G = grasslands, RL = rainfed arable land, IL = irrigated arable land, P = permanent crops, S = shrublands, BL = barren land, WI = wetlands and inland waters. For codes of EFTs see Table 1: capital letters correspond to the NDVI-I level, ranging from *A* to *D* for low to high NDVI-I. Small letters show the relative range, similarly ranging from *a* to *d* for low to high RREL. The numbers indicate the season of maximum NDVI.

obtained in other areas (see above) and the gradients interpreted from the CAs are consistent with the relative importance of productivity and phenology shown in our PCA. The strong contrast at the biogeographical regional level between the Eurosiberian and Mediterranean portions of Iberia underlie the variation in ecosystem responses observed, and is related to the bioclimatic control on the NDVI signal described by Lobo *et al.* (1997).

In addition to the spring and summer NDVI maxima described by Lobo *et al.* (1997), we found areas showing autumn and early winter absolute maxima, which were associated largely with low values of RREL (Figs 4 and 6). Our results for the month of the maximum NDVI (MMAX) agree with the phenological map of green-up onset (the beginning of the growing season) derived from MODIS by Peñuelas *et al.* (2004). However, it is important to note that primary production and NDVI may not be correlated seasonally if there is asynchrony between the seasonal dynamics of incoming photosynthetic active radiation (PAR) and the fraction of PAR absorbed (fAPAR). Under such conditions fAPAR or NDVI (the spectral linear estimator of fAPAR) should not be a linear estimator of seasonal primary production (Piñeiro *et al.*, 2005). Such asynchrony in some Mediterranean areas would be related to the evergreen nature of vegetation, to the winter distribution of precipitation and to the relatively mild temperatures in the coldest months of the year. Such conditions determine a displacement of the greenness onset and the date of the maximum to the autumn–winter months.

The NDVI curve does not provide a full description of ecosystem processes but captures essential features of the carbon and water cycles (Sellers *et al.*, 1992, 1996; Paruelo *et al.*, 1997, 2001b; Running *et al.*, 2000). Therefore, as a surrogate for radiation interception or carbon gains, it constitutes an integrative descriptor of ecosystem functioning (McNaughton *et al.*, 1989; Virginia & Wall, 2001).

We must be aware of the limits of NDVI to approximate terrestrial vegetation activity (e.g. influence of soils in arid environments or saturation over 0.7; Zhang *et al.*, 2004). However, as Xiao and Moody (2004) have pointed out, 'AVHRR/NDVI data currently provide our best empirical device for approximating spatio-temporal variability in terrestrial plant productivity at large scales'.

Identification of ecosystem functional types

The knowledge of the temporal and spatial patterns of ecosystem functioning at the regional scale provides a proper background to assess the effects of environmental changes (Gitay & Noble, 1997). Also, from regional to global scales, the definition of ecosystem functional types (EFTs) is an alternative to quantify functional diversity based on attributes related to processes that operate over large scales. Here, the ecosystem functional classification performed was established upon a simple three-dimensional histogram partition based on NDVI attributes derived from NOAA/AHRR-PAL images. Our goal was not centred on maximizing the variance among classes but on representing the spatial heterogeneity in functioning. Four intervals for each attribute were consistent with the four seasons of temperate ecosystems and kept a relatively low number of potential classes (64). A different number of intervals would have produced more concise or general results. Therefore, a change in the histogram partition or in the variables included may change the perception of the heterogeneity of the Iberian Peninsula. In fact, the same happens when different criteria or functional dimensions are used to define PFTs (e.g. lignin content; grasses, forbs, shrubs and tress; herbaceous vs. woody species).

Except for biophysically impossible combinations (high NDVI-I and high seasonality), almost any pattern of seasonal dynamics

of radiation interception is represented in the Iberian Peninsula. The lack of an EFT with high productivity and seasonality (*Dd*) reflects a physical constraint: if RREL is high, the ecosystem must have a low NDVI during part of the year, which in turn will reduce NDVI-I. On the other hand, an EFT with high productivity and low seasonality (*Da*) requires a high and stable NDVI throughout the year. For this reason, ANPP was the highest under low seasonality circumstances. This pattern occurred under summer NDVI maxima in the lowest parts of the Eurosiberian Region and in high Mediterranean mountains. It was also observed in some parts of the Eurosiberian–Mediterranean transition, the eastern Pyrenees and the western front of the Peninsula between the Tajo and Duero rivers, but in this case with autumn and early winter maxima. In addition, few Mediterranean areas in the southwestern part of the Peninsula were highly productive and barely seasonal. Mediterranean evergreen oak forests of southwestern Iberian Peninsula (Sierra del Aljibe), with relatively mild temperatures and under one of the highest precipitation regimes of Iberia, showed similar dynamics to subtropical ecosystems (Iguazú subtropical forest: 26° S, 54° W) (Paruelo *et al.*, 2001a; Garbulsky & Paruelo, 2004), not constrained by either low temperature or water availability.

EFTs with low productivity always had moderate to high seasonality, as in watered ecosystems or in the major river basins and semiarid areas of southeastern Iberia. In these cases, maximum values of NDVI were reached in summer and spring, respectively. The remaining part of the Mediterranean Region showed moderate productivity and seasonality and had maxima mainly in the autumn and early winter months. This was very common in the Mediterranean mountains.

Functional vs. structural ecosystem classifications

We did not attempt to assimilate the functional classes to the structural ones. Different potential vegetation and land-cover types had the same NDVI dynamics and, conversely, there were different functional dynamics within the same potential vegetation or land-cover unit. Most of the Iberian vegetation has been profoundly modified, so the lack of a total correspondence between functional and potential vegetation categories may simply reflect the difference between potential and current vegetation. It is also possible that some EFTs represent transitions between, rather than typical examples of, different vegetation units, or that several of the functional types defined here were part of a larger or smaller potential vegetation unit at a different aggregation level. Functional and structural classification schemes differed in the criteria used to define the level of aggregation of the units and to set boundaries between them. In this sense, the definition of boundaries between classes, either structural or functional, may change because of the observation protocol, i.e. seasonal dynamics of NDVI vs. vegetation physiognomy or land-cover (Allen & Hoekstra, 1992), setting a limit to the total correspondence between both descriptions. On the other hand, while we used the same aggregation criteria in classifying every pixel, the aggregation level varies among potential vegetation types. Also, remote sensing-based EFTs avoided scaling-up local observations to the region (Paruelo *et al.*, 2001a) and did not rely on models of the relationship between structural attributes and environmental features (bioclimate, soils etc.), scarcely tested at regional scale (e.g. Nielson *et al.*, 1992; but see Stephenson, 1990).

Nevertheless, results from the CAs discriminated the importance of both potential vegetation and land-use in explaining the functioning of particular ecosystems and some narrow correspondences were found. EFTs *Da1*, *Db1*, *Da2*, *Ca1* and *Cc1*, 22% of the Iberian Peninsula surface, were associated with potential vegetation, which indicates a higher bioclimatic control over the functioning of these areas. Conversely, human land-uses were more important in explaining the functioning of EFTs *Bb2*, *Bc2*, *Bc4* and *Bd3*, 15% of the Iberian surface. Modification of ecosystem functioning is a well-described consequence of human land use in many areas of the world (e.g. Paruelo *et al.*, 2001; Williams *et al.*, 2004), and has been associated frequently with an increase in seasonality (Paruelo *et al.*, 2001b; Guerschman *et al.*, 2003). In fact, agricultural land-uses of Iberia were related to EFTs with intermediate NDVI-I and high RREL.

As stated above, the definition of EFTs is dependent on the variables included. Remote sensing may provide additional functional variables to improve ecosystem descriptions (Nemani & Running, 1997). Shortwave albedo and surface temperature, two variables linked closely to the exchange of energy of the ecosystem, may provide a complementary description to the one presented here, based on the seasonal dynamics of carbon gains (e.g. Piñeiro *et al.*, 2002; Garbulsky & Paruelo, 2004). Besides, the integration of dissimilar phenological cycles from different PFTs or vegetation components occurring in an AVHRR-PAL pixel may be responsible for the observed NDVI dynamics (Schmidt & Karnieli, 2000). In spite of the spatial heterogeneity of Iberia, the NOAA/AVHRR-PAL data set provided a functional classification that retained ecological meaning. However, a more detailed study based on AVHRR-LAC or MODIS imagery will provided a more in-depth characterization of ecosystem functioning and its relationship with dominant PFTs, potential vegetation, bioclimate and land-use.

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BIOSKETCHES

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/geb

Appendix S1 The three Normalized Difference Vegetation Index (NDVI) attributes employed in the functional characterization of the Iberian Peninsula ecosystems (NDVI-I, RREL and MMAX).

Appendix S2 Main potential vegetation types of the Iberian Peninsula.

Appendix S3 Results of the correspondence analyses (CA) carried out between ecosystem functional types (EFTs) and (a) potential vegetation and (b) land covers.