

Factors affecting forest dynamics in the Iberian Peninsula from 1987 to 2012. The role of topography and drought

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ABSTRACT

In southern Europe, climate trends are expected to be characterized by an increase in temperatures and less water availability. Analyzing the role of structural factors and the influence of a changing climate provides insights into the evolution of forest ecosystems in regions with similar environmental conditions. The Mediterranean fringe of the Iberian Peninsula is of particular interest due to its diverse topographic climatic conditions and the increase in drought episodes during the last decades. This work studies forest dynamics in large areas of this geographical region by analyzing nine forest transitions. Vegetation covers were classified from three Landsat scenes for the period 1987–2012, and sub-periods 1987–2002 and 2002–2012. Conditions were described by topography derived variables, human factors and drought-occurrence variables. Boosted regression trees were used to identify the most important variables and describe the relationships between the forest dynamics and key factors. Variables such as solar radiation, topographic wetness index and tolerance to drought have been shown to be key factors in forest succession and when comparisons are made between vegetation groups. Main findings: The transition rate to Mediterranean and sub-Mediterranean broadleaf forests has increased during the analyzed period, while the transition rate to coniferous forests has decreased; Transitions to Mediterranean and sub-Mediterranean broadleaf forests are positively associated with drought occurrence while transitions to conifers are negatively affected by drought; Transitions from shrublands to forest stages are more vulnerable to factors controlling water availability; Important interactions between topography derived variables and drought have been found. The study provides robust evidence that drought occurrence plays an important role in the decline of conifers and the expansion of broadleaves, which could become the dominant species in many areas of the Mediterranean if climate model forecasts are met.

1. Introduction

Vegetation disturbances affecting all biome types have been observed in recent decades at global and continental scales (Hansen et al., 2013). Therefore, precise knowledge of the factors controlling vegetation dynamics is essential for improving ecosystem monitoring. For this purpose, analyzing vegetation transitions can provide significant insights, both from a methodological perspective and due to the findings.

The use of aerial photographs is an approach that is used widely in these studies, especially when a large coverage of historical aerial imagery is available. This approach has made it possible to obtain detailed information about vegetation types and changes in their spatial pattern over periods of 40–50 years (Allen et al., 1998; Sluiter and de

Jong, 2007; Alados et al., 2004). However, human-aided mapping is a time consuming task when large areas are under study, which is essential for defining regional or global trends. This is especially important for analyzing climate-induced vegetation shifts because it is necessary to cover a spatially representative area (Martínez-Vilalta and Lloret, 2016). In this sense, the broad scale of national forest inventories has made it possible to identify transitions between species at a regional scale (Coll et al., 2013; Vayreda et al., 2016; Monleon and Lintz, 2015), although the density of plots and the period covered between surveys (~10 years) mean that definitive conclusions about climate-driven vegetation shifts cannot be made (Martínez-Vilalta and Lloret, 2016). Finally, the use of remote-sensing techniques is considered the most appropriate approach for identifying robust trends in

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vegetation dynamics both spatially and temporarily (McDowell et al., 2015). Land-cover mapping based on satellite imagery can provide massive datasets (Wulder et al., 2008; Hermosilla et al., 2016; Vidal-Macua et al., 2017), although special attention should be paid to the possible uncertainty of these products (Pons et al., 2003, 2014; Pontius et al., 2004; Álvarez-Martínez et al., 2010) in order to obtain reliable land-cover change products and to avoid, as far as possible, the inclusion of noisy observations in the statistical analysis. The NASA-USGS Global Land Survey dataset (Gutman et al., 2013), primarily comprised of Landsat images (30 m resolution), is a very important resource for ecosystem monitoring from 1972 to present. Nevertheless, complementary methods are required to determine the proximate causes of large vegetation changes (McDowell et al., 2015).

In the Mediterranean mountains of Spain, ecological succession of vegetation has advanced after a general abandonment of traditional activities (García-Ruiz, 1990; Lasanta-Martínez et al., 2005; Jimenez-Olivencia et al., 2006; Cohen et al., 2011). Land-use management and, in general, human activities have been, and continue to be, the main driving force in the vegetation dynamics (Pino et al., 2000; Lasanta-Martínez et al., 2005; Gehrig-Fasel et al., 2007; Améztegui et al., 2010). However, other factors have to be taken into account to understand the vegetation colonization processes more fully as well as the shifts between species and between entire plant communities. The spatial pattern derived from the topography is a structural factor that explains much of the vegetation distribution. Interactions between topography-derived variables, such as altitude, slope, solar radiation or topographic effect on hydrological processes, are some of the factors most widely used in differentiating vegetation patterns (Pons and Solé-Sugrañes, 1994; Florinsky and Kuryakova, 1996; Burrough et al., 2001; Allen et al., 2004; Bennie et al., 2006; Serra-Díaz et al., 2011; Moeslund et al., 2013). The role of fire occurrence is another important issue for analyzing vegetation spatial-patterns and stability of certain plant communities (Díaz-Delgado and Pons, 2001; Salvador et al., 2005; Pausas and Keely, 2009). Climatic factors are also known to be main determinants in vegetation distribution, and climate dynamics are considered to drive vegetation shifts in many areas of the world (Walther et al., 2002; Schuur, 2003; Kelly and Goulden, 2008). In the Iberian Peninsula there has been a marked increase in temperatures and a decrease in precipitations over the last decades (López-Moreno et al., 2010; del Río et al., 2011, 2012; El Kenawy et al., 2012), which has led to an increase in the severity of droughts, especially in the Mediterranean area (IPCC, 2007, 2013; Gonzalez-Hidalgo et al., 2009; Vicente-Serrano, 2014; GECC, 2016). The response of vegetation to droughts has become a matter of growing interest (Breshears et al., 2005; Allen et al., 2010; Vicente-Serrano et al., 2013; Martínez-Vilalta and Lloret, 2016; Norman et al., 2016) and recent works have shown the effects of drought on several Mediterranean and European species (Bigler et al., 2006; Weber et al., 2007; Pasho et al., 2011; Camarero et al., 2011; Carnicer et al., 2011; Vilà-Cabrera et al., 2013; Galiano et al., 2013; Lévesque et al., 2013; Vicente-Serrano et al., 2015). Some of these species represent southernmost populations in the Mediterranean ambit, which explains their vulnerability to the warmer conditions (Andreu et al., 2007; Sánchez-Salguero et al., 2016). Declines of these species in forests could lead to long-term shifts (Peñuelas and Boada, 2003; Rigling et al., 2013; Galiano et al., 2010) and drought-tolerant species could become dominant in community compositions. The carbon stock of forests can be affected by these vegetation shifts (Vayreda et al., 2012), and the changes in flammability of vegetation can influence the fire regime, which is a very important issue in southern Europe (Pausas and Fernández-Muñoz, 2012; Moreira et al., 2012; Ganteaume and Jappiot, 2013).

Here, we analyze the influence of a series of physical, climatic and human factors on the forest dynamics in the Iberian Peninsula from 1987 to 2012. Two sub-periods have been included in the analysis, 1987–2002 and 2002–2012, in order to take into account the variability in human and climatic factors. The study focuses on progressive

succession (Glenn-Lewin et al., 1992) and forest transitions, analyzing the response to factors in nine different forest cover changes, from shrublands to shifts in mature developing stages between conifer, broadleaf evergreen and broadleaf deciduous forests. For this purpose we have selected three large representative ambits, taking into account their particular climatic context and topographic characteristics. These ambits correspond to refined land-cover classifications of three entire Landsat scenes (~32,400 km²). A set of variables derived from the SPEI (Standardized Precipitation-Evapotranspiration Index) was determined for spatially quantifying the occurrence of droughts. As far as we know, this is the first time that drought-occurrence variables have been used as explanatory factors of vegetation transitions.

Usually, the relationship between the explanatory variables and a given land cover transition is determined by linear regression analysis, such as logistic or multiple logistic regression (Serneels and Lambin, 2001; Serra et al., 2008), or by less commonly used approaches like Markov chains (Balzter, 1999). In our case, the importance of variables and how they influence each of the nine forest cover changes was analyzed using boosted regression trees (BRT), also known as stochastic gradient boosting (Friedman, 2001, 2002; Hastie et al., 2009). This relatively new machine-learning technique (Breiman, 2001), in which hundreds or thousands of decision trees (Breiman et al., 1984) are sequentially and progressively fitted, has been demonstrated to be particularly suited to predicting species distributions (Kawakita et al., 2005; Elith et al., 2006, 2008, 2009; De'ath, 2007; Leathwick et al., 2006; Crase et al., 2012) for the following main reasons: this approach does not assume any data distributions or data models, rather it tries to determine dominant patterns by combining many classification trees; it identifies relevant variables and complex interactions; it is much less influenced by correlated information or irrelevant variables than other statistical approaches; it produces stable predictions (variance reduction); and it provides graphical depictions of the relationship between the response variable and predictors. A separate BRT model was developed by forest cover change, period and study ambit, meaning that 81 models were evaluated.

The use of BRT is relatively new in ecology (Leathwick et al., 2006, 2008; Moisen et al., 2006; Sankaran et al., 2008; Levers et al., 2014; Verkerk et al., 2015), but we believe that they have not yet been applied to analyze vegetation transitions. Finally, we would like to highlight the particular relevance of the three study areas in the Iberian Peninsula: the three ambits are located on the Mediterranean fringe of the Peninsula, where a drying trend has been observed over the last decades, especially in the northeast (De Luis et al., 2010). Our intention was to provide insights into the conditions that lead to forest succession and transitions between vegetation groups, focusing on topographic variables, human-derived factors and drought occurrence. Thus, the main objectives of this study were to determine the following: (1) the most important factors in each of the forest cover transitions; (2) the role of the key factors for comparisons of the main forest species; (3) whether drought occurrence influences succession stages and forest transitions; and 4) whether drought occurrence has a clear influence, to determine the main interactions with other key factors.

2. Material and methods

2.1. Study areas

Three areas of Spain were included in this study as different scenarios for model development. Ambits correspond to land-cover classifications of three entire Landsat scenes, identified by their path-row: 198-031, 199-031 and 200-034 (Fig. 1). These large study areas were chosen because of their heterogeneity of biogeographical regions, including Alpine, Eurosiberian and Mediterranean areas, and, as previously explained, due to their climatic context. Representative mountainous regions of northeast and southeast Spain are included in these areas.

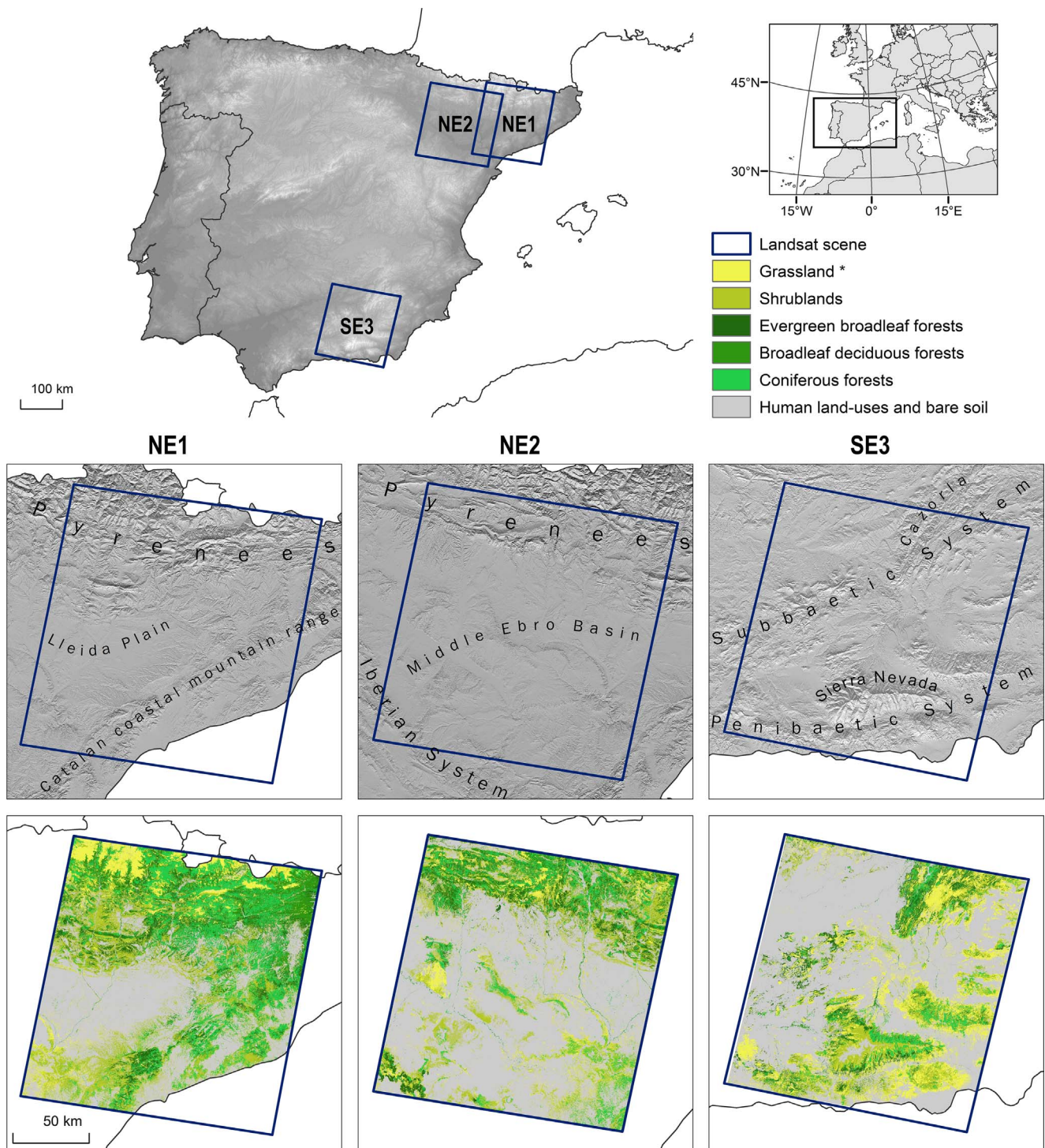


Fig. 1. Study areas. * Grassland category includes semi-arid and mountain ecotypes, and may include scattered shrubs or trees.

Scenes 198-031 and 199-031 are located in the northeast of the Iberian Peninsula and referred to hereafter as ambits NE1 and NE2 respectively. These two areas are spatially contiguous but have different environmental features, mainly because NE2 is more continental and arid. In addition, there is abundant reference information for these areas and some studies that can be related to ours.

The eastern ambit NE1 is influenced by a Mediterranean climate on the coast as well as the Catalan coastal mountain range, and by a continental climate in the Lleida Plain (Ebro basin) and Pyrenees (although the eastern Pyrenees also have a Mediterranean influence). Vegetation land-covers occupy a broad altitudinal range (from 0 to

3300 m), from sites near the coast to sites in the alpine and subalpine zones of the Pyrenees. Ambit NE2 has a greater continental influence in the Pyrenees and northern slopes of the Iberian System, with a semi-arid influence in the Middle Ebro Basin. In this ambit, which has less altitudinal range (from 50 to 2500 m), vegetation extends up to the upper montane zone and a very narrow area of the subalpine zone.

Scene 200-034 is located in southeastern Spain, and is hereafter referred to as ambit SE3. The coastal mountains in this ambit have a Mediterranean climate with pronounced aridity: less precipitations and higher temperatures than the northeastern ambits. Mountainous massifs of the eastern Baetic System, like the Sierra Nevada and Cazorla

mountain range, have a continental climate also with higher temperatures than the northern ambits. The Sierra Nevada has a complete altitudinal zonation, while there are environments from foothills to upper montane areas in most of these mountains.

2.2. Vegetation types

The study analyzes transitions between four vegetation classes derived from the land cover classification: shrublands, coniferous forests, broadleaf evergreen forests and broadleaf deciduous forests. The land cover class shrublands includes several formations ranging from temperate-xerophytic and temperate to alpine climate regions. Evergreen broadleaf sclerophyllous and evergreen needleleaf species are generally dominant in these areas (either as early transitional or permanent stages such as maquis). On the other hand, broadleaf deciduous shrubs are only dominant as permanent stages in cold-limited alpine environments. Coniferous forests are mainly composed by *Pinus halepensis*, *Pinus nigra* and *Pinus sylvestris*. In northern areas, *P. halepensis* is the dominant Mediterranean coniferous species below the upper montane zone, and in the southern area it is mixed with *P. nigra*, which, together with *P. sylvestris*, reaches the upper forest limit. Above the lower montane zone, Eurosiberian coniferous forests are composed mostly of *P. sylvestris*, with *P. nigra* at the lower limit and *Abies alba* and *P. uncinata* in the middle and upper areas (subalpine zone) respectively in the northern ambits. Broadleaf evergreen forests are dominated by *Quercus ilex* in the three ambits, although *Quercus coccifera* is widespread in NE2. *Q. ilex* extends from sites near the coast to the upper montane limit, and *Q. coccifera* spreads as continentality increases. Broadleaf deciduous forests are mainly composed by *Quercus pubescens*, *Quercus faginea* and *Fagus sylvatica*. *Q. pubescens* and *Q. faginea* are the dominant species below the upper montane zone in northern ambits, although in ambit NE2 they have a more patchy distribution. In the southern ambit, these species together with *Quercus pyrenaica* are restricted to sheltered locations. In the northern ambits, *F. sylvatica* is the most important Eurosiberian broadleaf deciduous species, although it is not present in subalpine zones.

2.3. Obtaining and refining land-cover maps

Vegetation cover maps were obtained by classifying Landsat imagery at 30-m resolution following the methodology described in Vidal-Macua et al. (2017). In our case, the k-nearest neighbor (kNN) classifier was used to obtain both multi-temporal training and test areas and to use them in final classifications. Each land-cover map refers to a five-year period, so classifications are composed of a set of dates in which the central years are 1987, 2002 and 2012. Training and test areas were extracted from the Land Occupation Information System of Spain 2005 (SIOSE, Sistema de Información sobre Ocupación del Suelo en España), a spatial database developed at a 1:25,000 scale (<http://www.siose.es/>). The disaggregation level of vegetation categories in the SIOSE database was used to determine the four vegetation classes defined in Section 2.2, except the grassland cover which is not included in the present work. Once a first set of SIOSE polygons were selected, we implemented a filtering process based on NDVI (Normalized Difference Vegetation Index) thresholds to reduce confusion between categories within polygons (Vidal-Macua et al., 2017). In a second stage, the kNN algorithm was applied to identify training and test pixels with an invariant statistical pattern for the 1987–2012 period (Vidal-Macua et al., 2017). Once these pixels had been identified for three dates, we used them as the final set to train the classifier and validate the results. The overall accuracy was greater than 90% for all three dates and ambits. The producer accuracy and user accuracy of vegetation land cover classes are shown in Table S1 of the Supplementary Material.

In order to avoid, as far as possible, including misclassified pixels in the statistical analysis, classifications were filtered using a confusion index (Burrough et al., 1997, 2000; Lewis et al., 2000; Gorsevski, 2005;

Tapia et al., 2005; Álvarez-Martínez et al., 2010). This index was calculated with the kNN algorithm in which the nearest training pixels (k-nearest neighbors) to each target pixel (to be classified) are identified by means of the Euclidean distance. Class membership values (M_c) are assigned to each target pixel according to the number of times a category C appears within the nearest training pixels (N_c) weighted by the squared inverse distance, following the expression:

$$M_c = \frac{\sum_{i=1}^{N_c} w_{ci}}{\sum_{i=1}^{N_k} w_{ci}}$$

where C is a land-cover category within the nearest training pixels and W is the inverse of the squared distance between the target pixel (x) and a training pixel (x') labeled with the class C : $W = 1/d(x, x')^2$; and N_k is the number of k nearest training pixels. Thus, a target pixel has a membership value for each land-cover category within the k nearest training pixels. Vidal-Macua et al., (2017) describes the procedure for determining the optimum value of k .

Finally, the uncertainty associated with a target pixel was calculated with the confusion index (CI) equation:

$$CI = 1 - (M_c \max_1 - M_c \max_2)$$

where $M_c \max_1$ is the maximum membership value of land-cover categories within the k nearest training pixels, and $M_c \max_2$ is the second maximum membership value.

Values of this index range from 0 to 1, so that values close to 1 indicate high confusion between at least two classes, and values close to 0 represent high certainty for a classified pixel. We used a threshold of 0.5 so that pixels classified with a CI over this value were masked to exclude them from the land-cover maps.

A second mask was created to remove misregistration in land-cover polygon boundaries. These situations are related to the location inaccuracy of border pixels after the geometric correction, and therefore, to false positive or negative changes between land-cover classifications (Pons et al., 2003). To solve this, classification polygon boundaries were eroded with a 20-m buffer mask according to the average RMS error of the imagery geometric correction. More details about this methodology can be found in Pons et al. (2003).

As our work is focused on natural ecological succession, we also used a mask to remove forest plantation areas, extracted from the SIOSE (Land Occupation Information System of Spain) database. Burned areas (REDIAM, 2016; Gobierno de Aragón, 2016; Generalitat de Catalunya, 2016) in each period were also masked. Like wildfires, insect outbreaks and windstorms are other important disturbances; however, in our analysis we focus on isolating, as much as possible, the influence of topography, drought and other variables described in later chapters on forest dynamics.

Finally, classifications were overlaid to obtain 9 forest-cover changes (Table 1) for the periods 1987–2012, 1987–2002 and

Table 1
Forest cover transitions.

Initial land-cover	Land-cover change	Code
Shrublands to	Coniferous forests	1. SRB-CNF
	Broadleaf evergreen forests	2. SRB-BEF
	Broadleaf deciduous forests	3. SRB-BDF
Coniferous forests to	Broadleaf evergreen forests	4. CNF-BEF
	Broadleaf deciduous forests	5. CNF-BDF
Broadleaf evergreen forests to	Coniferous forests	6. BEF-CNF
	Broadleaf deciduous forests	7. BEF-BDF
Broadleaf deciduous forests to	Coniferous forests	8. BDF-CNF
	Broadleaf evergreen forests	9. BDF-BEF

2002–2012. These transitions define the 9 models for each ambit and period; however, as explained below, some models were removed due to their low number of observations. In the present work, transitions from shrublands to forest stages are related to early development stages, so in later sections this term will be used to refer to these transitions (SRB-CNF, SRB-BEF and SRB-BDF in Table 1).

2.4. Sampling

We considered land-cover changes as absence/presence events. Areas where the initial land-cover remained stable between two dates were treated as absences, and those where there were changes in land-cover were treated as presences. For instance, absence areas (no-change events) in shrubland to coniferous forest cover are those where shrubland polygons in 1987 and 2002 match; and presence areas (change events) are those where shrubland polygons in 1987 and coniferous forest polygons in 2002 match, and so on for each land-cover change and period.

Once the change and no-change areas were established, stratified random sampling was carried out, attempting to maintain the prevalence (the same number of points) between the two types of events. As a general rule, 3000 points were randomly selected for each event class with a minimum distance of 250 m between each point. Prevalence was not achieved in all cases, especially in the southern ambit, where certain vegetation formations, like broadleaf deciduous forest, lack dynamism (compared with other formations) due to climatic conditions and the rear-edge location. In these cases we kept the resulting proportions between presences and absences since it has been shown that BRT models perform well with unbalanced samples (Edith et al., 2008; Sankaran et al., 2008; Edith and Graham, 2009; Crase et al., 2012). Nevertheless, extremely unbalanced models were rejected (see Section 3). Each dataset (composed by 6000 points when there is prevalence) was randomly split into two subsets, one made up of 75% of the samples for fitting the model, and a validation subset with the remaining 25% of samples.

2.5. Explanatory variables

In order to interpret the forest transitions, a set of variables was chosen (Table 2) to be included as explanatory factors in the models.

Table 2
Explanatory variables.

Variable code	Description	Units
Altitude	Altitude	Meters
Slope	Slope	Degrees
Curv	Overall terrain curvature	Dimensionless
Pf_Curv	Profile curvature	Dimensionless
Pl_Curv	Plan curvature	Dimensionless
VRM	Terrain roughness	Dimensionless
TWI	Topographic Wetness Index	Dimensionless
Win_SRad	Winter solar radiation	10 kJ m ⁻² day ⁻¹
Sum_SRad	Summer solar radiation	10 kJ m ⁻² day ⁻¹
Wind	Wind	Meters/second
Lithology	Acidity or basicity of the geologic substrate	Categorical
Dist_UrbA	Euclidean distance to urban areas	Meters
Dist_SecRo	Euclidean distance to secondary roads	Meters
Dist_MajRo	Euclidean distance to major roads	Meters
PopDen	Population density	Inhabitants/km ²
Pop_Dyn	Population gain or loss	Categorical
Liv_Units	Livestock units	Livestock units
S6_80_02_5 (example)	Every drought variable is coded as follows: "S6" – First two digits indicate the SPEI time-scale (6 or 24) "80_02" – Span of years used to calculate drought occurrence "5" – Last digit indicates drought episode duration	Number of drought episodes

The intention was to identify the most important variables and use statistical inference to describe the likelihood of a forest-cover change according to the value range of the variables. The MiraMon 8.2, ArcGis 10.1 and SAGA 2.1.2 software were used to calculate these variables.

2.5.1. Topography-derived variables

These variables are related to physical and environmental factors that could influence vegetation succession and competition within forest stages. The intention was to determine how the different vegetation types adapt to the environmental variability derived from the topography and to identify what vegetation types are more dynamic or vulnerable in the different topo-climatic contexts.

A 10 m DEM was created from 1:5000 map sheets of the Aerial Orthophotography National Plan 2010 (PNOA) and the following variables were derived from it:

- Altitude in meters above sea level.
- Slope in degrees.
- Terrain curvature (dimensionless), which includes overall curvature, profile curvature (in the slope direction) and plane curvature (perpendicular to the slope direction). The 0 value means no curvature in a typical range from -5 to 5, where negative values represent concave curves and positive values indicate convex curves.
- Terrain roughness (dimensionless), using the Vector Ruggedness Measure (Sappington et al., 2007), for which values close to 0 represent flat areas in an approximate range from 0 to 0.20 in our ambits.
- Topographic Wetness Index (dimensionless), which is a DEM-based soil moisture index (Beven and Kirkby, 1979; Sørensen et al., 2006; Kopecký and Čížková, 2010), and generally ranges from 3 to 30, where higher values indicate higher moisture availability.
- Winter and summer solar radiation (units in 10 kJ m⁻² day⁻¹), which computes the total amount of incident solar radiation for each pixel at winter and summer solstice dates, following the methodology of Pons and Ninyerola (2008).

2.5.2. Wind

Wind data came from the Webservice-Energy platform (<http://www.webservice-energy.org/>) and CENER (National Renewable Energy Centre), and refer to mean wind speed in meters per second in a 4-km resolution raster. Wind can be a restrictive factor to plant growth and can influence seed dispersal.

2.5.3. Lithology

Lithology data may refer to the acidity or basicity of the geologic substrate. After obtaining geological information layers from several institutions (Spain, Catalonia, Aragon and Andalusia Governments) we reclassified the lithological groups into the following classes: acidic, basic and mixed. This is related to the tolerance of vegetation to low pH (silicates, more abundant in acidic rocks) or high pH (carbonates, more common in basic rocks).

2.5.4. Distance variables

Three variables were obtained as a measure of landscape accessibility: Euclidean distance to urban areas (cities, towns and villages), Euclidean distance to major roads, and Euclidean distance to secondary roads. We used the same road network and urban areas layers (obtained from the same governmental institutions) to create these variables for all periods, firstly because we did not find information about building dates or any other older layers, and secondly because we assumed that there has been few changes in the entirety of these infrastructures. We relate this variable both to the influence of isolation from infrastructures on forest management abandonment, and to the possible disturbance in natural dynamics due to higher accessibility.

2.5.5. Municipality-level information

Three variables were elaborated from INE (Spanish Statistical Office) data at a municipality level as factors that can disturb the natural succession:

- Population density (inhabitants per square kilometer). The central year of each analysis period was chosen as the reference year. Changes in this variable and in population dynamics could influence vegetation re-growth (Parcerisas et al., 2012).
- Population dynamics. The population gain or loss was calculated between each pair of dates of an analysis period. Four classes were defined as follows: $\geq 50\%$ (and less than 100%) population increase, $\geq 100\%$ population increase, $\geq 33\%$ population decrease and no relevant changes.
- Livestock units, which account for cattle, sheep, goats and horses. Extensive and stabled livestock are placed in a single category in the INE data. Extensive livestock is more widespread in mountain areas where vegetation cover changes are taking place. This activity can affect vegetation succession, especially in shrubland covers, but also in evergreen forests because goats and sheep eat the acorns of *Quercus ilex*. In general terms, during 1987–2012, livestock units have increased by approximately 40% in the southern ambit and have not varied significantly in the northern ambits, although different trends can be found depending on the municipality.

2.5.6. Variables representing recurrent drought episodes based on the standardized precipitation evapotranspiration index

A set of variables indicating recurrent drought episodes was generated based on the Digital Topo-climatic Drought Atlas of the Spanish Iberian Peninsula (Domingo-Marimon, 2016). The Atlas includes a set of SPEI (Standardized Precipitation-Evapotranspiration Index) maps at 100-m spatial resolution for the entire Iberian Peninsula from 1950 to 2012. The SPEI (Vicente-Serrano et al., 2010a), based on precipitation and mean temperature (to estimate potential evapotranspiration), is an index that quantifies water deficits for multiple timescales. The values are standard deviations for which negative values indicate less than average precipitation, i.e. drought events, while positive values indicate greater than average precipitation, i.e. wet events. A threshold of $\text{SPEI} = < -1$ is selected to identify drought conditions, which end as soon as $\text{SPEI} > -1$ again.

The index was computed at several timescales corresponding to drought specific conditions. A first set of variables was generated using SPEI at a 6-month timescale from 1980 to 2012 as indicative of the medium-term moisture condition, which first identifies anomalies in the water streamflow. A second set of variables was generated using SPEI at a 24-month timescale from 1980 to 2012 as indicative of the long-term moisture condition, which identifies reservoir level and ground water level anomalies. For both sets, the number of drought episodes ($\text{SPEI} = < -1$) with durations of a minimum of 4, 5, 7 or 8 consecutive months, as representative lengths that may cause harmful effects, were counted for the period 1980–2012. The number of drought episodes was also counted by year spans of 15, 10 and 5 years for the 1987–2012 period. Therefore, the year spans used were: 1980–2012, 1997–2012, 2002–2012 and 2007–2012. In addition, the analysis was performed using two shorter sub-periods, 1987–2002 and 2002–2012, and their corresponding year spans: 1980–2002, 1987–2002, 1992–2002, 1997–2002, and 1980–2012, 1997–2012, 2002–2012 and 2007–2012 respectively. Including several year spans allows us to analyze how a greater or lesser drought frequency influences forest dynamics and whether recent droughts (during the last 5–10 years) have had an effect on transitions. The final dataset consisted of 32 drought variables in each model.

2.6. Variable subset selection

A collinearity analysis was carried out before the models were run

to avoid the presence of correlated quantitative variables and to reduce processing times. The initial set of 49 variables was resized for each model using an alternative way to correlate coefficient estimates. We used Variance Inflation Factors (VIF) and a VIF threshold of 5 as other authors recommend (Zuur et al., 2009; O'Brien, 2007; James et al., 2013). The analysis begins by making a regression of each variable on the other variables, and then calculating the VIF value: $VIF = 1/(1-R^2)$; where R_i^2 is the R^2 of the regression of a variable onto all other variables. High values of R^2 (close to 1) mean that a variable is correlated with one or more variables, which in turn will lead to a high VIF value. After that, the variable with the highest VIF is removed. The analysis continues iteratively, recalculating VIF with the regressions of the remaining variables, until all variables have a $VIF \leq 5$.

2.7. Data analysis

To identify the most important variables and to quantify their influence on forest transitions we used boosted regression trees (BRT), also known as stochastic gradient boosting (Friedman, 2001; Friedman, 2002; Hastie et al., 2009). BRT is a tree-based method combined with the strength of boosting (Breiman et al., 1984; Hastie et al., 2009; James et al., 2013). Classification trees segment the value range of an explanatory variable in order to determine regions that maximize the occurrence probability of a class inside them. Several variables can be combined to construct a tree depending on the interactions between them; for instance, from a tree of a single variable with a cutpoint and two regions, to a more complex tree where one of these regions can be split into two subregions based on a cutpoint in a second variable. The algorithm finds the best candidate variables in order to minimize the error rate while looking for a tree complexity that reduces the variance and the risk of overfit (James et al., 2013). The random forest algorithm (Breiman, 2001) is a substantial improvement over decision trees because it introduces bagging (Breiman, 1996) as a procedure for reducing variance and the error rate. By bagging, many bootstrapped samples (in the order of hundreds or thousands without replacement) are selected randomly from the training set to fit the same number of trees using a different random subset of variables in each of them (Hastie et al., 2009; James et al., 2013). The prediction for each observation is the average over all models.

Boosting (Freund and Schapire, 1996; Ridgeway, 1999; Friedman, 2002) is the optimization method in BRT. Like bagging, in the boosting algorithm hundreds or thousands of trees are built using a random fraction of the observations (without replacement) in each new tree. The main difference is that trees are not fitted individually but additively because each new tree is fitted to the residuals of the previous tree. The procedure to sequentially build trees is based on a series of rules that weigh observations depending on their error rate after fitting the previous tree (Friedman, 2002; Hastie et al., 2009). Each new tree is focused then on observations that have been poorly predicted.

2.7.1. Model fitting and evaluation

The procedure followed for fitting the BRT models is described in Section S1 of the Supplementary Material.

The initial results showed that altitude is the variable that contributed most notably in most models, so we fitted an additional model that did not include this predictor. The altitude variable can be interpreted as a climatic variable because it introduces a temperature and precipitation gradient. We assumed that variables interacting with altitude are more likely to be selected as important contributors, so removing it would allow other interacting schemes to fit the models.

2.7.2. Model inference

To interpret the results in each forest transition model, we determined the importance of the predictors in the BRT models by considering their contributions in the additive model. The relative importance was measured based on the number of times a predictor was

selected for splitting, weighted by the squared improvement to the model as a result of each split, and averaged by the number of trees (Friedman and Meulman, 2003; Hastie et al., 2009). Then, results were scaled between 1 and 100.

The response of a forest transition in the predictor values was interpreted using partial dependence plots. This graphic output shows the relationship between the response and an explanatory variable after the average effects of all other variables are accounted for, using the weighted tree traversal method described in Friedman (2001) (Ridgeway, 2004). Thus, these plots depict where the suitable conditions are for a transition to take place. Some interactions between variables are shown using three-dimensional partial dependence plots (Elith et al., 2008), which are based on predictions for each variable pair.

3. Results

3.1. Model validation

Information about the model validation is provided in Section S2 of the Supplementary Material.

3.2. Estimate of the transition rate between vegetation types (summary)

Although most of the area corresponded to zones that remained stable, there are some trends which are worth highlighting. In the northern ambits (Tables S5 and S6), while the percentage of change towards coniferous forest has decreased from one period to the next in all transitions, transition rates towards broadleaf evergreen forest have increased (except in the BDF-BEF transition), especially in ambit NE2. In these ambits, the transition rates towards broadleaf deciduous forest have also increased, although to a lesser degree. On the other hand, in the southern ambit (Table S7) all transition rates have decreased from one period to the next, especially in CNF-BEF shifts.

3.3. Explanatory factors in forest cover changes

The collinearity analysis (VIF) allowed reducing models size. The variables removed were mainly drought indices (from an initial set of 32 to 12–14 drought variables). In most cases, summer solar radiation was removed in the VIF analysis. The relative importance of explanatory variables for each forest cover change, period and ambit is shown in Tables S8–S10 of the supplementary material. In order to synthesize the results, our analysis mainly focuses on the six most important variables in each forest cover change and ambit (Table 3). To do this, we calculated the average importance of each variable, considering the six most important variables in each period, including and excluding altitude. However, other variables were taken into account to improve species comparisons and the reliability of explanations. Partial dependence plots can be consulted in Figs. S19–S30. In general, topography-derived variables and drought indexes showed the clearest patterns; therefore, we emphasize the role of these variables when types of transitions are compared.

3.3.1. Transitions from shrubland to forest stages (SRB-CNF, SRB-BEF and SRB-BDF)

We have selected four topography-derived variables to compare changes from shrubland covers in the 1987–2012 period (Fig. 2): altitude, slope, solar radiation and soil moisture (TWI). A similar pattern for altitude can be detected in NE1 and NE2; however, given that the altitudinal range in NE2 has a lower upper limit, comparing trends from 1600–1700 m upwards could be misinterpreted. This pattern represents the altitudinal zonation of vegetation. Thermo and meso-Mediterranean conifers are more competitive on foothills (below 500–600 m) and Eurosiberian conifers above the lower montane zone (1400–1500 m). Broadleaf forests are more dynamic from the super-

Mediterranean zone (600–700 m) to the upper montane zone (1700–1800 m). Ambit SE3 shows similar patterns but with an upward shift due to a more xeric climatic context. For this reason, succession to upper-montane conifers (*Pinus sylvestris*) are less likely events than in northern ambits, and transitions to broadleaf deciduous are very rare ones.

In all cases, locations with lower solar radiation are more suitable, although SRB-CNF dynamics seem to be more tolerant to higher solar radiation. All transitions are dependent on soil moisture (TWI), especially in transitions to broadleaf forests in northern ambits.

There are significant findings with respect to drought indices. In ambit NE1, long-term drought occurrence negatively affects SRB-CNF changes, which are more likely at sites where the SPEI at a 24-month timescale and at least 8-month duration occurs at most once (Figs. S19 and S21). On the other hand, medium-term droughts (SPEI at a 6-month timescale) of 4 and 5-month duration have a positive influence on transitions to broadleaf evergreen forest (SRB-BEF) in northern ambits (Figs. S21 and S25). We identified important interactions regarding these indices, and some examples are shown in Fig. 3. In ambit NE1, SRB-BEF transitions are occurring at sites more affected by drought events, low wind velocity and low solar radiation values (Fig. 3A). The same interaction regarding solar radiation can be seen at ambit NE2 together with high TWI values (Fig. 3B).

Drought occurrence also has a positive influence on SRB-BDF changes in ambit NE1. In this case medium-term drought events occurred during the last five years (2007–2012) (Fig. S21). Looking at the most important drought variables, SRB-BDF transitions are more likely at sites affected by, at least, 1–2 occurrences of medium-term droughts of 8-month duration and at sites affected by 3–4 occurrences of medium-term droughts of 4-month duration. We used reference information (Catalonia Land-Cover Map 1:25,000, 2009) to calculate the average distance between SRB-BDF presence events and vegetation cover polygons according to the dominant species (Table S11 of supplementary material). We found that the closest species were *Pinus sylvestris* and *Quercus pubescens*, thus, the latter is a more drought-tolerant species. The most important interactions with drought occurrence are again variables that can influence the water evaporation (Fig. 4), although medium-term droughts of 4-month duration show less pronounced interactions.

3.3.2. Transitions between conifer and broadleaf evergreen species (BEF-CNF and CNF-BEF)

We have selected the following variables to analyze forest transitions: altitude, slope, solar radiation, soil moisture (TWI) and wind. The response to variables in shifts between conifers and broadleaf evergreen species are shown in Fig. 5. In general, broadleaves are better adapted to steep slopes, which is also reflected in the other forest transitions. As in the previous section, patterns concerning altitude can be easily interpreted by relating them to the altitudinal zonation of vegetation groups. In ambit NE2, higher probabilities of BEF-CNF shifts are concentrated above the lower montane zone, where conifer species are mainly composed of *Pinus sylvestris*. In northern ambits, BEF-CNF shifts are more likely to occur as solar radiation decreases, especially in ambit NE2. In NE1, the “u” shape in the dependence on soil moisture plot (TWI) could reflect the presence of the two types of conifers in BEF-CNF shifts: *P. halepensis*, which is more adapted to lower values, and *Pinus sylvestris*, which is more dependent on water availability. In NE2, *P. sylvestris* is more dynamic than evergreen *Quercus* spp. as solar radiation decreases and TWI increases. Unlike in ambit NE1, shifts to evergreen *Quercus* spp. (CNF-BEF) in ambit NE2 are more likely as solar radiation increases and seem to be more tolerant to soil water scarcity. On the other hand, in ambit SE3, the density of presence events and probability regarding the altitude indicate that Mediterranean conifers are predominant in BEF-CNF transitions. This ambit does not show remarkable differences regarding solar radiation. Instead, response to soil moisture shows that CNF-BEF transitions are more likely than

Table 3

The six most important variables by forest cover change and ambit. M.I.V = Most important variables; Freq. = frequency (number of times the variable is within the 6 most important variables); A.R.I = Average relative importance. The following models were not used in the analysis due the scarcity of presence events: BDC-CNF in the 2002–2012 period in NE2, and CNF-BDF and BDF-CNF in three periods in SE3.

	Ambit NE1			Ambit NE2			Ambit SE3		
	M.I.V.	Freq.	M.R.I.	M.I.V.	Freq.	M.R.I.	M.I.V.	Freq.	M.R.I.
SRB-CNF	S24_07_12_8	4	19.56 ± 1.27	Wind	6	12.97 ± 1.78	Altitude	3	20.53 ± 1.74
	Altitude	3	17.39 ± 1.20	Altitude	3	9.08 ± 1.41	Slope	6	9.04 ± 2.65
	Liv_Units	2	7.61 ± 0.34	Liv_Units	6	8.98 ± 0.90	Liv_Units	6	7.88 ± 1.88
	PopDen	6	7.51 ± 0.90	PopDen	6	7.44 ± 1.07	Wind	6	7.50 ± 1.43
	Slope	4	6.56 ± 1.64	Dist_MajRo	6	7.26 ± 0.51	Dist_MajRo	6	7.46 ± 0.99
	Wind	6	6.28 ± 0.93	Win_SRad	4	7.09 ± 0.48	PopDen	3	7.37 ± 1.26
SRB-BEF	Altitude	3	29.01 ± 11.37	Altitude	3	41.18 ± 12.51	Altitude	3	26.71 ± 3.02
	Win_SRad	6	11.54 ± 1.87	S6_80_02_5	1	17.11 ± 0	Win_SRad	4	8.97 ± 1.01
	S6_80_02_4	1	8.97 ± 0	Win_SRad	4	9.65 ± 3.30	Lithology	1	8.74 ± 0
	Wind	5	6.95 ± 2.53	S6_80_12_5	1	8.59 ± 0	Dist_MajRo	6	7.96 ± 1.31
	Liv_Units	2	6.67 ± 0.82	PopDen	2	8.50 ± 1.22	Dist_UrbA	2	7.72 ± 2.21
	VRM	6	6.20 ± 1.49	VRM	3	7.33 ± 0.11	PopDen	6	7.17 ± 0.80
SRB-BDF	Altitude	3	33.86 ± 6.29	Altitude	3	20.49 ± 1.52	Altitude	3	22.53 ± 2.15
	S6_07_12_8	2	14.91 ± 3.83	Wind	6	11.34 ± 3.52	TWI	6	13.09 ± 4.56
	S6_07_12_4	2	10.46 ± 6.57	Win_SRad	6	10.78 ± 3.09	S6_07_12_5	1	12.43 ± 0
	Liv_Units	5	8.64 ± 4.20	TWI	5	10.64 ± 1.77	S6_80_02_5	1	11.77 ± 0
	Win_SRad	6	8.47 ± 1.77	PopDen	6	9.67 ± 2.51	Dist_MajRo	4	7.62 ± 1.42
	S6_97_02_8	1	8.23 ± 0	Dist_MajRo	3	6.66 ± 1.78	S6_07_12_4	2	7.54 ± 1.32
CNF-BEF	Altitude	3	32.02 ± 1.91	Altitude	3	24.42 ± 11.95	Altitude	3	15.47 ± 1.14
	Win_SRad	6	9.41 ± 2.13	Wind	6	10.85 ± 1.48	Dist_MajRo	6	9.56 ± 0.47
	Wind	5	7.30 ± 1.30	Dist_MajRo	6	7.11 ± 1.36	Wind	6	8.81 ± 2.31
	Slope	6	7.29 ± 0.78	PopDen	4	6.95 ± 1.44	Dist_UrbA	6	8.33 ± 1.40
	S6_80_12_7	1	6.86 ± 0	Win_SRad	5	6.51 ± 0.96	Liv_Units	3	7.28 ± 1.85
	Liv_Units	5	6.43 ± 1.79	Dist_UrbA	5	6.32 ± 0.53	PopDen	3	7.04 ± 0.39
CNF-BDF	Altitude	3	17.79 ± 3.70	Altitude	3	18.04 ± 10.48			
	Liv_Units	6	9.66 ± 3.11	Slope	6	14.07 ± 3.54			
	S6_07_12_8	4	8.27 ± 0.86	Win_SRad	6	11.58 ± 3.70			
	Slope	6	8.04 ± 1.24	Lithology	5	11.26 ± 4.84			
	PopDen	2	7.39 ± 0.50	PopDen	6	8.04 ± 1.90			
	Wind	2	7.31 ± 1.12	Wind	3	6.84 ± 3.06			
BEF-CNF	Slope	6	14.55 ± 0.37	S24_97_02_8	2	14.97 ± 0.60	Slope	6	11.14 ± 1.81
	Win_SRad	6	9.30 ± 0.70	Wind	6	11.23 ± 0.87	Altitude	3	10.85 ± 3.20
	Altitude	3	8.82 ± 0.80	S6_92_02_4	2	11.19 ± 1.32	Liv_Units	6	9.26 ± 0.98
	Wind	6	7.49 ± 1.03	Altitude	3	10.14 ± 4.71	Dist_MajRo	6	8.83 ± 0.90
	Liv_Units	3	6.87 ± 0.96	Slope	6	9.36 ± 2.56	Wind	1	7.31 ± 0
	S24_07_12_7	1	6.62 ± 0	Dist_MajRo	4	8.30 ± 0.70	Dist_SecRo	2	6.93 ± 1.04
BEF-BDF	Win_SRad	6	14.34 ± 4.91	Win_SRad	6	18.45 ± 6.74	Lithology	6	23.97 ± 7.25
	PopDen	3	9.28 ± 3.97	Altitude	3	11.38 ± 2.59	Dist_UrbA	6	11.72 ± 6.35
	S6_07_12_8	1	8.78 ± 0	Wind	6	9.37 ± 4.09	TWI	6	9.42 ± 2.40
	Liv_Units	6	8.61 ± 0.77	Slope	6	9.00 ± 4.25	Altitude	3	9.24 ± 3.57
	Slope	4	7.43 ± 0.83	Liv_Units	2	5.66 ± 0.05	Slope	4	7.03 ± 0.63
	Wind	5	6.99 ± 1.05	Dist_MajRo	5	5.50 ± 0.99	Wind	3	6.71 ± 1.11
BDF-CNF	Altitude	3	20.70 ± 14.88	Dist_MajRo	4	14.09 ± 9.18			
	Slope	6	10.93 ± 1.12	Altitude	2	11.95 ± 2.96			
	Dist_SecRo	1	10.09 ± 0	Slope	4	11.02 ± 1.82			
	Liv_Units	4	9.73 ± 2.43	Liv_Units	2	9.29 ± 0.70			
	VRM	4	9.61 ± 2.23	Dist_UrbA	4	7.98 ± 0.85			
	Wind	3	8.51 ± 2.05	Wind	4	7.64 ± 2.05			
BDF-BEF	Altitude	3	24.05 ± 2.16	Win_SRad	4	16.25 ± 0.93	Altitude	3	32.41 ± 4.52
	Liv_Units	6	10.70 ± 3.53	Altitude	3	10.69 ± 1.42	Sum_SRad	3	9.34 ± 3.63
	Win_SRad	5	9.44 ± 1.36	Slope	6	9.22 ± 1.08	Liv_Units	1	9.06 ± 0
	Slope	5	9.17 ± 2.85	Wind	6	8.68 ± 0.96	Dist_UrbA	4	8.85 ± 2.79
	Wind	6	7.00 ± 1.21	Dist_UrbA	1	8.16 ± 0	Dist_MajRo	6	8.60 ± 3.37
	PopDen	3	6.69 ± 0.48	PopDen	1	7.40 ± 0	Wind	4	8.23 ± 0.89

BEF–CNF as TWI values increase. Wind velocity does not show clear patterns; however, the lower wind velocities seem to be more suitable for *Pinus sylvestris* and evergreen *Quercus* spp. in NE2 and SE3 respectively.

Shifts between conifers and broadleaf evergreen species show significant associations with drought variables. BEF–CNF transitions in ambit NE1 are more likely at sites where long-term droughts of at least 7-month duration occurs at most once (Fig. S20). In ambit NE2, these

shifts are more likely when long-term droughts of at least 8-month duration do not occur (Figs. S24 and S26). In addition, occurrence of medium-term droughts of 4–month duration in NE2 (Figs. S24 and S26) seems to be less suitable for BEF–CNF transitions. Changes from conifers to evergreen *Quercus* spp. (CNF–BEF) in ambit NE1 are associated with a decrease in the number of occurrences of medium-term droughts of 7–month duration (Fig. S21). It is worth noting that, unlike in NE1, this shift in NE2 is more likely as occurrences of medium-term droughts of

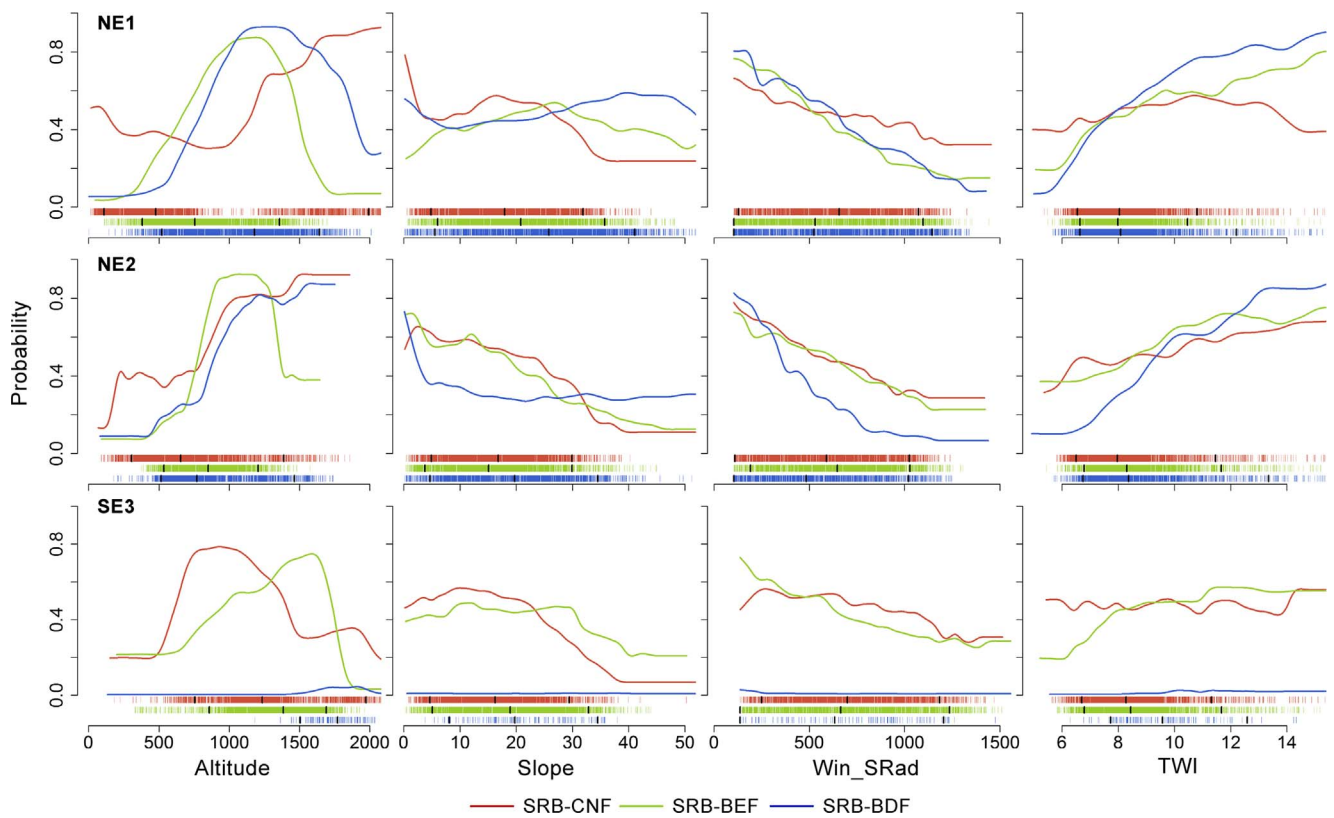


Fig. 2. Response of SRB-CNF, SRB-BEF and SRB-BDF transitions to altitude, slope, solar radiation and soil moisture (TWI) for the three ambits in the 1987–2012 period. Density of presence events is represented by vertical lines above the x-axes, and overlaid solid black ticks depict the 0.05, 0.5 and 0.95 percentiles.

5-month duration increase (Fig. S25). We have plotted the response of CNF-BEF to different drought durations, which can be compared in the two northern ambits (Fig. 6). A similar pattern between ambits can be observed in terms of density of observations (vertical bars). In terms of suitability, patterns match well if we consider that a very low number of observations in B3 with high probabilities at 5–6 repetitions can be related to small statistical artifacts (derived from the method used to interpolate climatic data or classify land-cover) or exceptional topoclimatic conditions. This suggests that, the greater importance of slope in ambit NE1 (Table S8), compared with NE2 (Table S9), could explain the greater importance of the drought of 7-month duration in NE1 and its negative effects.

3.3.3. Transitions between conifer and broadleaf deciduous species (BDF-CNF and CNF-BDF)

For transitions between conifers and broadleaf deciduous species we can only report the results for the northern ambits (Fig. 8) because these models were rejected in ambit SE3 (Table S4). We kept the dependence curve of BDF-CNF shifts in ambit NE2 although it is a less reliable model for establishing comparisons because it is a more unbalanced sample (Table S3). CNF-BDF shift patterns differ markedly in response to altitude. We found out that higher probabilities below 500 m in ambit NE2 are related to the presence of an important anastomosed river (Cinca River) with extensive fluvial deposits where vegetation dynamics depend on stability and the age of deposits (Ojeda, 2007). Looking at the response to altitude in this ambit, *Fagus sylvatica* seems to be the species with most dynamism in CNF-BDF shifts (above 1500 m). Water evaporation is observed as an important factor in the dynamics between these species. Broadleaf deciduous species tend to progress as solar radiation decreases and soil moisture increases. In addition, lower wind velocities are more suitable for these species in NE1. In mixed landscapes of conifers and broadleaf deciduous species, the conifers are less vulnerable to solar radiation and more dynamic

with lower soil moisture values.

In contrast to vulnerability to soil moisture availability, medium-term droughts of at least 7–8-month duration have a positive association with CNF-BDF shifts in NE1 (Figs. S19 and S21). *Quercus pubescens* is the predominant broadleaf deciduous species in these transitions and *Pinus sylvestris* the coniferous one (Table S11). This is consistent with the partial dependence on altitude (Fig. 8), where there are higher probabilities in a range from 1000 to 1200 m. Thus, the results indicate that in mixed forests of these two species, *Quercus pubescens* is less sensitive to drought and this is reflected as a shift.

3.3.4. Transitions between broadleaf evergreen and broadleaf deciduous species (BDF-BEF and BEF-BDF)

Dynamics between broadleaf evergreen species and broadleaf deciduous species are shown in Fig. 9. Both transitions in SE3 and BDF-BEF transitions in NE2 correspond to more unbalanced samples, which is reflected in lower probabilities. In terms of the response pattern to variables, the common trend regarding the altitude is that BEF-BDF shifts are more likely above the lower montane zone and BDF-BEF shifts are more likely in foothills and Mediterranean zones. Tolerance to water evaporation is again a differential factor in these transitions. Broadleaf evergreen species are more dynamic than broadleaf deciduous species as solar radiation increases and TWI values decrease. Instead, broadleaf deciduous species are more dynamic on north faces and with soil moisture availability. Patterns in dependence to wind velocity are less clear, although BEF-BDF transitions seem to be more likely with low wind velocities.

Quercus pubescens is the most abundant broadleaf deciduous species regarding these transitions in NE1 (Table S11). This species again seems to show a positive association with drought occurrence in mixed landscapes with *Quercus ilex* under medium-term drought conditions (drought variable that contributed most: SPEI at a 6-month timescale and 8-month duration) (Table 3 and Figs. S20 and S22). It is worth

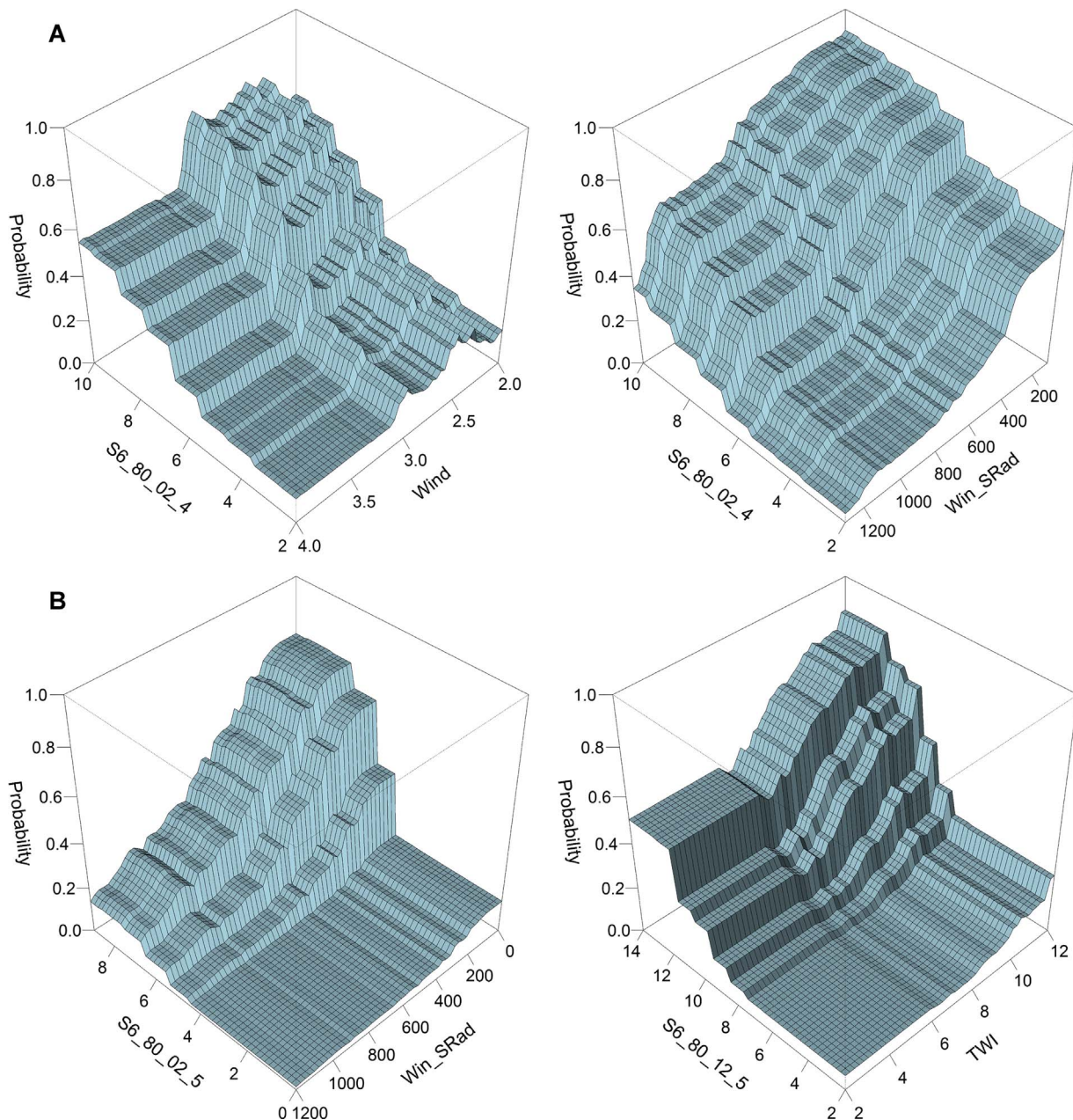


Fig. 3. Variables that interact with drought occurrence in SRB-BEF transitions: wind and solar radiation in NE1, 1987–2002 period (A); solar radiation and soil moisture (TWI) in NE2, 1987–2002 and 1987–2012 periods (B).

keeping in mind that solar radiation is the most important variable; therefore, looking at the response to this variable it is reasonable to presume that under medium-term droughts conditions *Quercus pubescens* is more dynamic in mixed forests on north faces.

4. Discussion

In general terms, transition rates derived from classifying the three Landsat scenes indicate that broadleaf forests have increased their area in the northern ambits, while coniferous forests have followed a declining trend from one period to the next, which is consistent with former studies (Vayreda et al., 2016, Carnicer et al., 2014). In contrast, the magnitude of the transitions in the southern region suggests that broadleaf evergreen species, like *Quercus ilex*, are becoming less dynamic, in agreement with Vayreda et al. (2016), who found a contraction of the latitudinal range of this species at its southernmost limit.

In addition, and in accordance with these authors, the expansion of evergreen broadleaves appears to be greater in the more xeric environments of the northern regions (NE2).

All transitions from shrubland are vulnerable to high solar radiation, indicating that water evaporation is a controlling factor in early stages of forest dynamics. Hence, soil water availability also increases recruitment, although coniferous species are more tolerant to low soil moisture values, and to higher solar radiation, which can be explained by the heliophilous character of pines (Blanco et al., 1997; Broncano et al., 1998, Ameztegui and Coll, 2011). It is reasonable to think that early developing stages are more dependent on topo-climatic conditions like soil moisture, which is driven by solar radiation and the TWI, among other factors. These results are in line with other studies reporting the susceptibility of seedling growth of the evergreen *Quercus* spp. (Espelta et al., 1995; Benayas, 1998) and *Pinus sylvestris* (Castro et al., 2004) to large evapotranspiration rates in open spaces and canopy gaps.

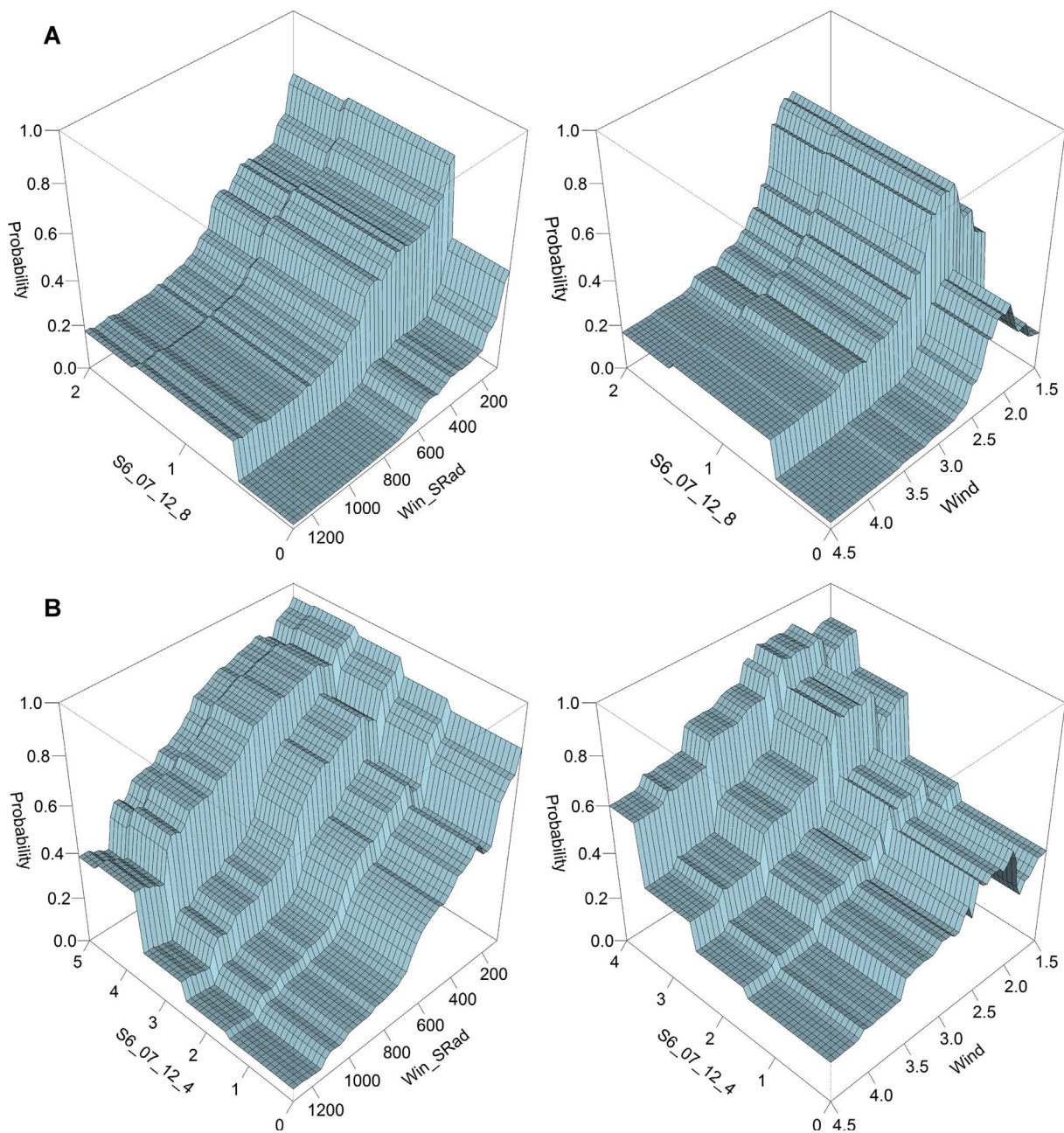


Fig. 4. Variables interacting with drought occurrence in SRB-BDF shifts, ambit NE1: solar radiation and wind in the 2002–2012 period (A); solar radiation and wind in the 1987–2012 period (B).

Concerning competition within forest stages, broadleaf deciduous species are the vegetation group that is most dependent on topographic factors controlling moisture retention (i.e. transitions to these species are more likely as solar radiation decreases and TWI values increase). Non-Mediterranean conifers, such as *Pinus sylvestris*, benefit from soil moisture retention and low solar radiation in competition with broadleaf evergreen species, which is clearly manifested in a drier environment such as the ambit NE2. On the other hand, Mediterranean conifers and broadleaf evergreen species do not show a clear preference regarding solar radiation. However, our results suggest that broadleaf evergreen species have a greater plasticity, as they are more competitive in a more xeric ambit with lower water availability (Fig. 5, ambit NE2) and under drought conditions (Fig. S29), which is in parallel with other works (Vicente-Serrano et al., 2010b, Pasho et al., 2011). Nonetheless, there is another factor that could influence these dynamics:

Quercus coccifera, which is more extended in NE2 than in NE1, has less water requirements than *Quercus ilex* (Blanco et al., 1997). Besides, our results corroborate that under warmer climate conditions (Fig. 5, ambit SE3), broadleaf evergreen species tend to be much more competitive with soil moisture availability (Blanco et al., 1997), also because its roots are able to penetrate into the deep water table (Lloret et al., 2004). In general, the more developed root system of broadleaves also explains their better adaptation to steep slopes.

Response to drought events has been shown to be an important driving factor in vegetation succession and forest shifts. The results suggest that under drought conditions, in mixed landscapes composed of Mediterranean and sub-Mediterranean broadleaves and conifers, shifts to broadleaves are more likely to occur. These findings are consistent with previous works showing that evergreen *Quercus* spp. are more adapted to drought periods than pines (Martínez-Ferri et al., 2000;

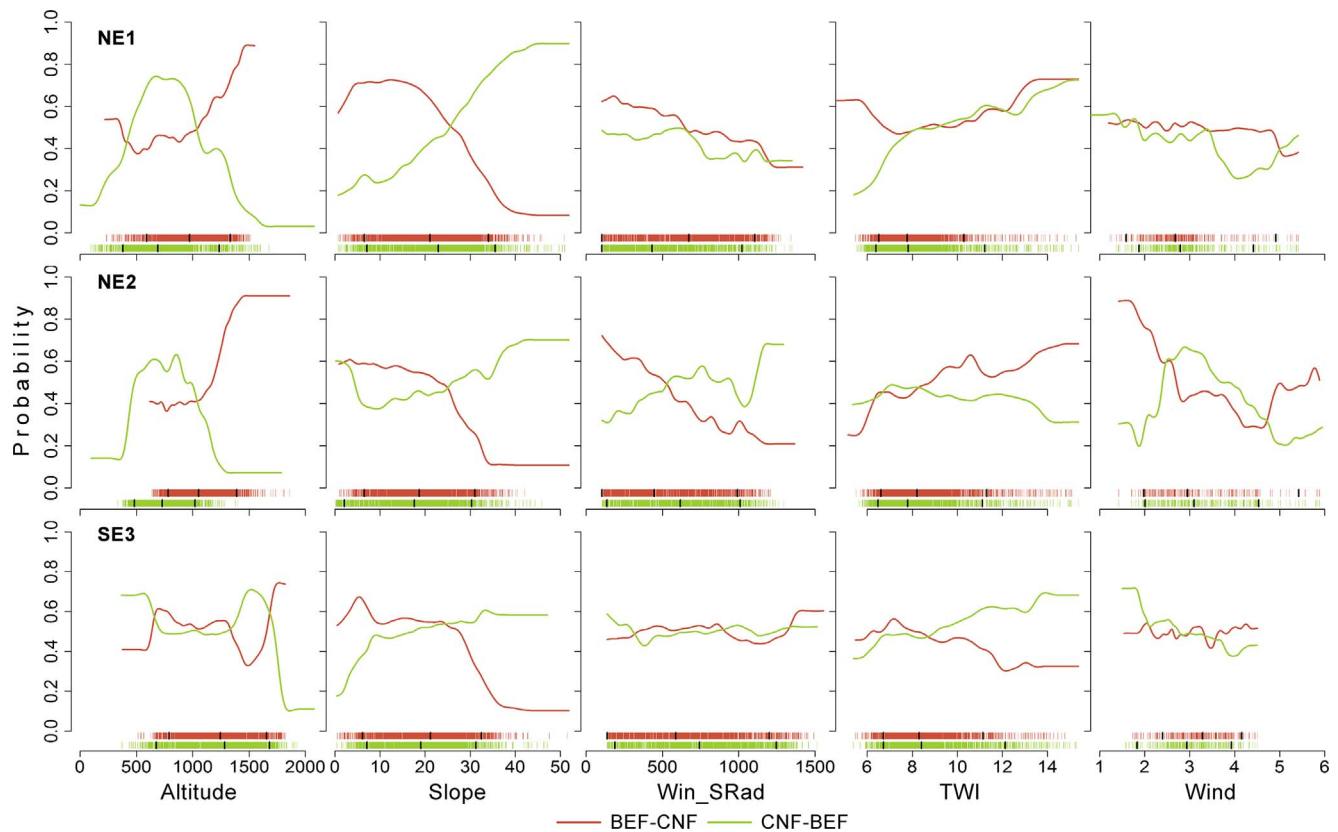


Fig. 5. Response of BEF-CNF and CNF-BEF transitions to altitude, slope, solar radiation, soil moisture (TWI) and wind, for the three ambits in the 1987–2012 period. The density of presence events is represented by vertical lines above x-axes, and overlaid solid black ticks depict 0.05, 0.5 and 0.95 percentiles.

Vicente-Serrano et al., 2010b; Pasho et al., 2011; Büntgen et al., 2013), especially in the case of *Pinus Sylvestris* (Bigler et al., 2006; Sánchez-Salguero et al., 2012; Vilà-Cabrera et al., 2013) which is in the southernmost populations of its distribution. The adaptive strategy of sclerophyllia in evergreen *Quercus* spp. and its larger and deeper roots suggest a greater resistance to water shortage. In the same line, other researches show that seedling and recruitment of *Quercus pubescens* (sub-Mediterranean broadleaf deciduous tree) benefits from drought conditions in mixed forests with *Pinus sylvestris* (Galiano et al., 2010, 2013; Rigling et al., 2013). This does not mean that broadleaves sprout as a consequence of drought. It is logical to suppose that they have been in the understory or that they were not the dominant species, and after canopy defoliation or tree dieback of *Pinus sylvestris*, the dynamics of broadleaves remain stable. Our study also points out that *Quercus pubescens* could be more dynamic than evergreen *Quercus* spp. under drought conditions (especially on north faces), supporting the results obtained in two works by Galiano et al., (2010, 2013). These authors reported the association between *Quercus* spp. seedling abundance and drought occurrence, and in both works they found that seedling recruitment of *Quercus pubescens* was significantly greater than *Quercus ilex*.

However, the interaction with topo-climatic factors must be taken into account when drought tolerance is analyzed. For instance, successions from shrubland towards Mediterranean broadleaf forests are driven by drought tolerance, but under favorable topo-climatic conditions of water availability (low solar radiation levels, high soil moisture values and low wind velocities), indicating that juvenile plants have narrower niches to withstand a disturbance event (Martínez-Vilalta and Lloret, 2016, Jackson et al., 2009). This is consistent with other works that reported the drought tolerance of *Quercus ilex* recruitment and seedlings, especially when soil water availability is not a limiting factor (Blanco et al., 1997; Benayas, 1998; Corcuera et al., 2004). On the other hand, evergreen broadleaves on very steep slopes are vulnerable to

longer droughts (Fig. 7), suggesting that the combination of abiotic stress effects reduces the competitive ability of these species.

Drought-induced vegetation decline has been reported as a global trend (Allen et al., 2010). The Mediterranean basin and particularly the Iberian Peninsula are geographical regions where defoliation and tree mortality of the main forest species are associated with the recent increase in drier conditions (Carnicer et al., 2011; Neuman et al., 2017). However, our results clearly suggest that broadleaves are better able to withstand drought disturbances; and that the observed decline in shifts to conifers could be driven by the increase in drought frequency, as is also reported for other regions (Mueller et al., 2005; Dolanc et al., 2013; McDowell et al., 2016). These forest dynamics may have effects on the carbon storage of Mediterranean forests because it has been proven that the increase in broadleaves in mixed forests with conifers enhances carbon sequestration (Vayreda et al., 2012). At the same time, and according to climate models (Giorgi and Lionello, 2008), long-term drought-induced vegetation shifts could have effects on fires, whose frequency and severity have increased in southern Europe during the last decades (Pausas et al., 2009; Moreira et al., 2011; Ganteaume and Jappiot, 2013). In this sense, some studies have shown that pines are more highly flammable than evergreen broadleaves (Ganteaume et al., 2011; Kauf et al., 2014), and there is evidence of lower fire hazard in mixed forests of broadleaves and pines and mature evergreen broadleaf forests than in pure pine forests (Fernandes, 2009; Moreira et al., 2009; Fernandes et al., 2010). On the other hand, Ganteaume et al. (2011) found a higher ignition frequency and shorter time-to-ignition in leaf litter of mixed stands composed of Mediterranean pines and broadleaves than in litter of pure pine stands.

We are aware that historical land management has had a strong influence on the vegetation dynamics in the Iberian Peninsula, and that land abandonment and the replacement of firewood by fossil fuels has contributed to the expansion of broadleaves (Vayreda et al., 2016). Nevertheless, the consistency that our approach provides, because it

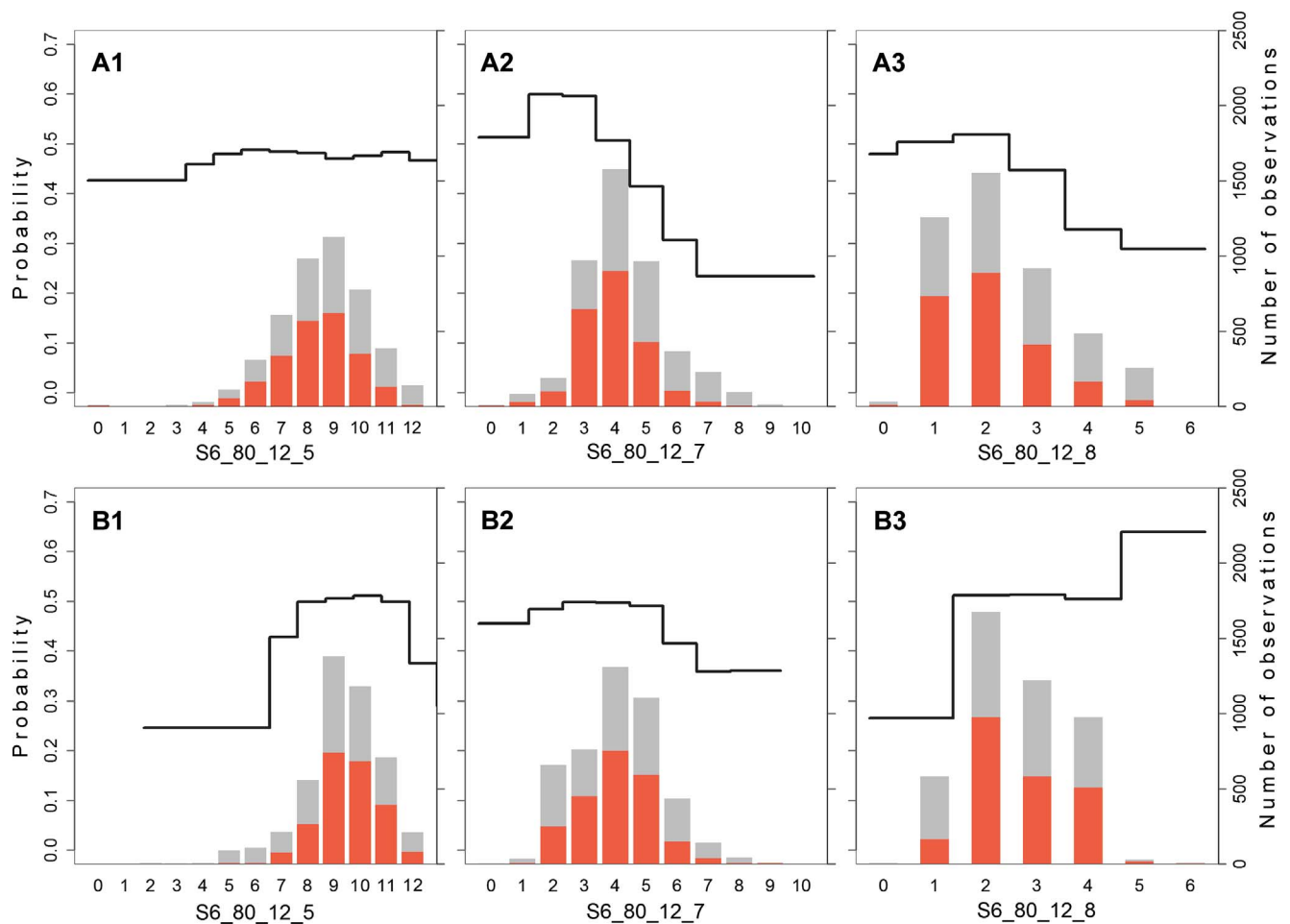


Fig. 6. Response of CNF-BEF transitions to different drought durations. A1-A3: ambit NE1, 1987–2012 period. B1-B3: ambit NE2, 1987–2012 period. Black solid line depicts occurrence probability and vertical bars depict density of observations in the training set by number of occurrences (presence events in red, absence events in grey).

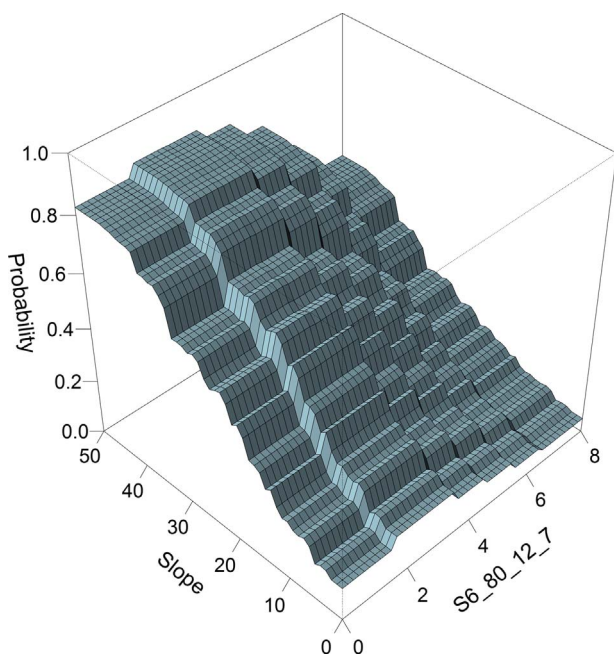


Fig. 7. Interaction between slope and the SPEI at a 6 month timescale and 7-month duration in CNF-BEF transitions, ambit NE1, 1987–2012 period.

covers a broad and diverse region and the robustness of BRT models, reinforces the idea that drought occurrence plays a very important role in vegetation shifts of this geographical region.

5. Conclusions

Forest transitions in three large areas of the Iberian Peninsula have been analyzed considering the role of several variables in vegetation groups dynamics, from early developing stages to successions within forest vegetation stages. Topography-related variables, such as solar radiation, soil moisture and slope, as well as drought tolerance have been shown as key factors in determining certain transitions. Drought occurrence has a negative influence on transitions to coniferous forest and a positive association with transitions towards Mediterranean and sub-Mediterranean broadleaf species. However, the study shows that interaction with topo-climatic factors, as well as drought duration, plays an important role in withstanding drought events.

Our work is in line with previous studies that indicate the vulnerability of species such as *Pinus sylvestris* (Martínez-Vilalta and Piñol, 2002; Galiano et al., 2013; Vilà-Cabrera et al., 2013; Sánchez-Salguero, 2016) to the increase in drier conditions predicted for the future (IPCC, 2013). Populations of this species in the Mediterranean area are situated at their southernmost limit, which may indicate that this limit is moving northwards due to recurrent droughts. This could lead to an expansion of Mediterranean and sub-Mediterranean *Quercus* spp. and

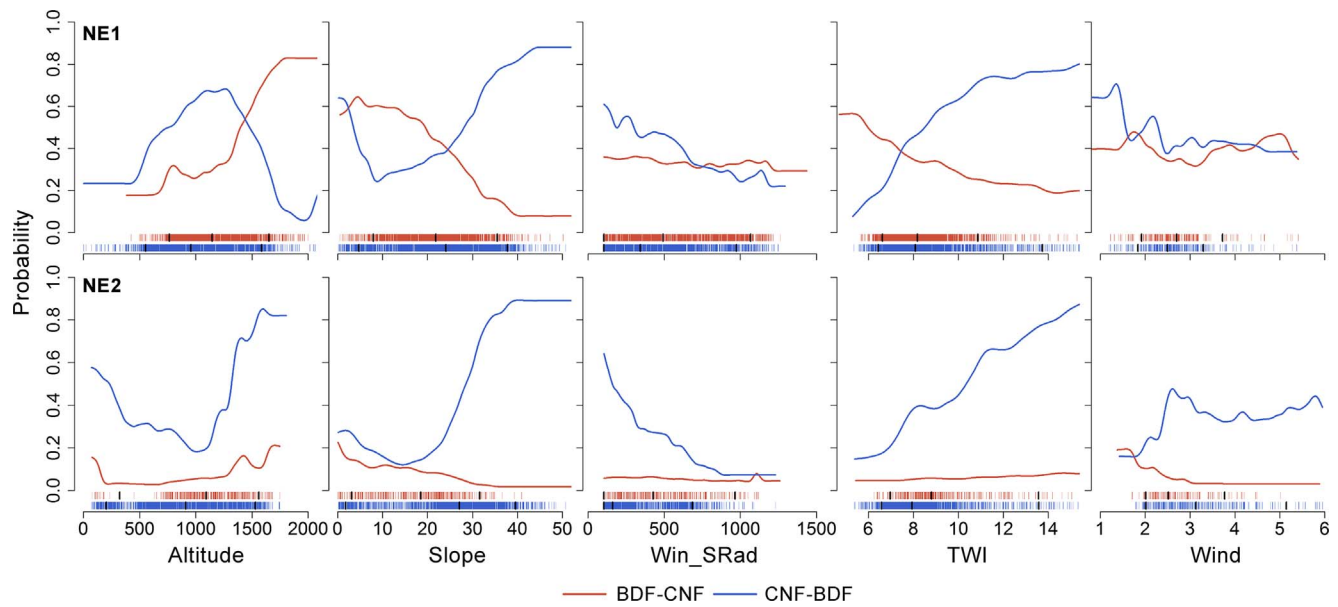


Fig. 8. Response of BDF-CNF and CNF-BDF transitions to altitude, slope, solar radiation, soil moisture (TWI) and wind, in ambits NE1 and NE2 in the 1987–2012 period. Density of presence events is represented by vertical lines above the x-axes, and overlaid solid black ticks depict 0.05, 0.5 and 0.95 percentiles.

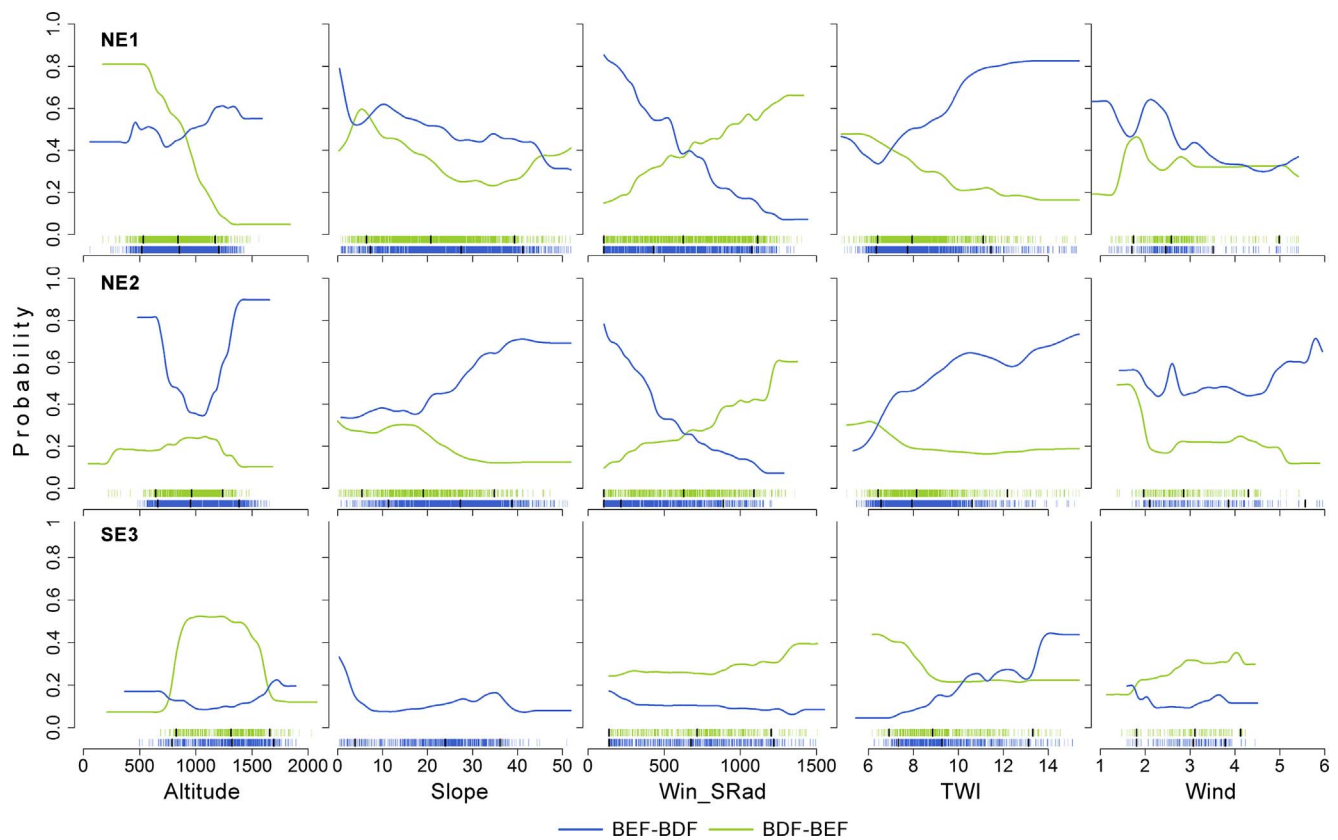


Fig. 9. Response of BDF-BEF and BEF-BDF transitions to altitude, slope, solar radiation, soil moisture (TWI) and wind, 1987–2012 period. Slope variable is not shown in BDF-BEF of ambit SE3 because after the VIF analysis it was removed. Density of presence events is represented by vertical lines above the x-axes, and overlaid solid black ticks depict 0.05, 0.5 and 0.95 percentiles.

an upward shift of their altitudinal range (Peñuelas and Boada, 2003; Gimmi et al., 2010; Vilà-Cabrera et al., 2013; Rigling et al., 2013; Vayreda et al., 2016). With these considerations, shifts detected in the present work should be monitored in future works to assess whether they are eventual shifts, stages of ecological succession, or shifts consolidated over time (as mature vegetation).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.10.011>.

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