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ORIGINAL ARTICLE

Spatial variation of wetland woods in the latitudinal transition to arid regions: a multiscale approach

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ABSTRACT

Aim In order to investigate the occurrence of wetland woods in the latitudinal transition to arid regions in south-western Europe, we studied species patterns (richness and abundance), examined floristic differences between woods along the latitudinal gradient, and determined the relative influence of the underlying environmental drivers of plant variation at various scales.

Location The Atlantic coastal belt of the Iberian Peninsula along the entire latitudinal gradient (44–38° N).

Methods Large-scale surveys were carried out in search of woods located in flats or depressions with prolonged waterlogging. Stands were selected for study when they displayed a continuous tree structure and little sign of human disturbance. Sampling included plant inventories in 114 plots, in which presence and abundance cover were recorded for all vascular and bryophyte species. Both diversity and composition were used to investigate plant species patterns. Gamma and alpha diversity (species richness) values were used to compare Ibero-Atlantic wetland woods with other European woods. Species richness was modelled as a function of environmental variation at regional and finer scales (landscape and local scale), using linear mixed-effects models and model selection based on the Akaike information criterion. Hierarchical clustering and ordination using perennial species were used to detect floristic differences between sites. Partial canonical correspondence analyses were performed to determine the relative importance of each set of environmental drivers in structuring the vegetation trends at regional and finer scales.

Results A significant proportion of wetland woods occurred in the transition to the Mediterranean region. Ibero-Atlantic wetland woods displayed low gamma and alpha diversity compared with other woods. Species richness was strongly influenced by finer-scale variables, in particular distance to rivers, whereas regional variables were less influential. Based on tree dominance, the classification revealed five vegetation types, but the majority of stands (86%) were included in woods dominated by *Salix atrocinerea* Brot. and *Alnus glutinosa* (L.) Gaertner. Species abundances were correlated with both regional and finer-scale hydrological variables, which explained 37.5% of the variation, 11.9% of which corresponded to regional and 18.5% to finer-scale environmental descriptors.

Main conclusions True wetland woods persist in the transition to arid regions of south-western Europe. The latitudinal gradient influences the spatial variation of species, but local hydrological variables were found to play a significant role in both diversity and compositional patterns.

Keywords

Akaike weights, alpha diversity, floristic composition, gamma diversity, Iberian Peninsula, local scale, ordination, regional scale, variation partitioning, wetland woods.

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INTRODUCTION

Processes governing regional and local species variation have been the focus of increasing ecological and biogeographical research interest in the past decade (Zobel, 1997; Whittaker *et al.*, 2001; Willis & Whittaker, 2002). It is becoming increasingly apparent that the factors that best account for species variation patterns are influenced by scale (Willis & Whittaker, 2002). However, the relative importance of each of these factors remains largely unknown (Hérault & Honnay, 2005). Community diversity has long been considered the outcome of local environmental heterogeneity and local ecological processes such as predation and competition (Ricklefs, 1987). Recent studies at the macro-scale have demonstrated that geographical gradients in the species (or genus or family) richness of plants, in particular woody plants such as trees and shrubs, can be viewed as by-products of water–energy dynamics – which is the fundamental climate-driving process (O'Brien, 2006). Both local and regional mechanisms with an influence on diversity are considered to interact in a continuum of time and space, establishing a relationship between regional and local diversity patterns (Ricklefs, 2004).

Interest in determining the relative roles of multiscale drivers in shaping plant assemblages has recently focused on floodplain ecosystems, particularly riparian ones (Mouw & Alaback, 2003; Hérault & Honnay, 2005; Renöfält *et al.*, 2005). Several hypotheses have been developed and tested, including the idea that dispersal along riparian corridors (Nilsson *et al.*, 1994) permits species exchange between regional and local species pools (Décamps & Tabacchi, 1994). The strong local–regional connection in species pools is thought to be responsible for the high plant diversity in river landscapes (Naiman & Décamps, 1997).

Most of this research has been undertaken in temperate zones, whereas few studies address the underlying multiscale floodplain ecosystem drivers in southern (both Mediterranean and Atlantic) European areas (but see Aguiar *et al.*, 2005). The particular water-stressed climatic conditions (low summer water levels and a high degree of seasonal and inter-annual variability) enhance the hydrographic network's role in the interchange of species between regional and local scales in such areas. Moreover, southern European areas are characterized by a long-lasting history of intensive land use, which has significantly modified the landscape (Médail & Quézel, 1999). Both the lateral and longitudinal continuities within the floodplain landscape have changed substantially since plant communities developed following the arrival and expansion of taxa after post-glacial migration (Brayshay & Dinnin, 1999). Floodplain forests probably covered extensive areas prior to human clearance for settlement and agriculture (Brown *et al.*, 1997). The present study is focused on the current remnants of the potentially larger floodplain forests of the Ibero-Atlantic area. These remnants display various degrees of connection with fluvial courses. They are located at varying distances from rivers, and some are completely isolated as a result of natural or human-induced history. In line with Kelly & Iremonger (1997) we defined these patches as wetland woods in the broad sense of the term, to include all woodlands on soils that are subject to flooding, waterlogging or markedly impeded drainage. Wetland woods are thus naturally inundated or saturated areas that support a significant component of woody vegetation adapted to poorly aerated and/or saturated soil (Lugo, 1990).

About 60% of Spain's wetlands disappeared during the second half of the 20th century (Hughes, 1995). Drainage and water diversion were probably the main factors that affected Mediterranean wetlands. Water that is naturally destined to support rivers and marginal wetlands is stored in reservoirs in upland valleys, diverted to irrigated agricultural land and urban developments, and excluded from floodplains (Dynesius & Nilsson, 1994; Nilsson *et al.*, 2005). Despite their ecological role and endangered status, there is no accurate estimate of the total area covered by wetland woods in the Ibero-Atlantic area (Brinson & Malvárez, 2002). Existing information refers to wetland inventories *sensu lato* (DGOH, 1991; Farinha & Trindade, 1994) or to studies of local wetland woods (Izco & Ramil-Rego, 2002). Wetland wood communities and their underlying drivers have received little attention in wetland or woodland studies (Kelly & Iremonger, 1997). Some of the existing definitions of wetland woods are included in general wetland classifications (Hughes, 1995; Semeniuk & Semeniuk, 1997), forest classifications (Peterken, 1993; Rodwell, 1998), or even in general studies on mires (Wheeler, 1984). Current wetland wood research involves phytosociological studies (Kelly & Iremonger, 1997; Prieditis, 1997; Amigo *et al.*, 2004).

Wetlands can occur under the driest climatic regimes if there is an available source of water that can maintain the water table close to the soil surface (Kroes & Brinson, 2004). However, given that a climate's capacity to support wetlands on floodplains diminishes above some threshold value of the potential evapotranspiration/precipitation ratio, whether or not there are true wetland woods in the southern parts of Iberia is open to discussion. As the study area comprises wetland woods located along a transitional gradient to arid regions, new questions arise as to the relative roles of multiscale processes in shaping species variation, and the extent to which fragmentation in southern floodplain forests and the subsequent isolation of remnant patches influence the interaction of regional and local species processes.

This study aims to investigate the occurrence and floristic specificity of wetland woods along the Atlantic coastal belt of the Iberian Peninsula. We aimed to answer two key questions: (1) what are the relative roles of the main environmental drivers of diversity and community structure of wetland woods, and (2) at which spatial scale(s) do these drivers operate along the latitudinal transition from temperate to arid climate?

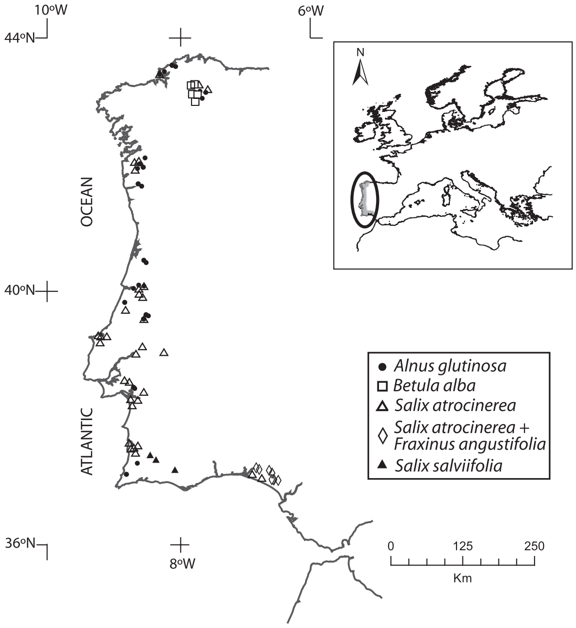


Figure 1 Western Europe, showing the study area and the location of the sampling sites (geographical coordinate system, Datum D_WGS_1984). Different symbols represent different floristic groups, considering canopy dominance.

MATERIALS AND METHODS

Species data

Extensive surveys were carried out during the summers of 2002, 2003 and 2004 in order to locate freshwater wetland wood stands along the entire latitudinal gradient (44–38° N) of the Atlantic coastal belt of the Iberian Peninsula, from north-western Spain to southern Portugal and south-western Spain (Fig. 1), between parallels 6 and 9° W. Surveys were based on field surveys and oral information from local botanists.

The criteria for stand selection included hydrological and floristic features: dense tree cover (> 70%) was required and > 25% of the forested area had to be waterlogged in summer, whatever the water source. We also looked for stands with little sign of human disturbance in either the stand itself or the surrounding area. Only 42 stands from the original surveys met these criteria and also possessed both varying degrees of soil moisture (hydroperiod) and mixed sources of water (surface and groundwater). These stands may well represent the last remnants of larger forests that once completely occupied the depressional valleys in which they occur (80% of the woods were < 10 ha in size).

The number of sampling plots per stand was based on the stand area and the environmental and floristic heterogeneity. The latter are a direct result of the area's microtopography, which influences patterns of water submersion and the formation of pools, backwaters and channels; plots were located in such a way as to reflect this variability. Plot size was large enough to be representative of both the overstorey and understorey vegetation (mean area, 174.5 ± 77.3 m^2) and to contain the most frequent species. A total of 114 floristic samples (plots) were taken (three to four plots per wood for most stands; see Appendix S1 in Supplementary Material for a description of the different wood stands). The presence and percentage cover of all vascular plants and bryophytes were estimated visually. Species that could not be reliably identified in the field were collected and identified at the LISI Herbarium (Instituto Superior de Agronomia, Lisboa). The nomenclature followed Castroviejo *et al.* (1986–2003) and Tutin *et al.* (1964–80). Voucher specimens were kept for the LISI Herbarium.

Environmental data

We considered abiotic drivers at the levels of region (regional scale), stand (landscape scale) and within-stand (local scale) (Appendix S2), based on the hierarchical framework for processes that influence biodiversity proposed by Willis & Whittaker (2002). The variables were classified as continuous (scores all numbers), discrete ordinal (classes) and binomial (true = 1/false = 0). Regional variables included geographical coordinates and a list of climatic data and bioclimatic indices (Appendix S2). Potential evapotranspiration was calculated following the Thornthwaite method (Thornthwaite, 1948). Bioclimatic indices were obtained using the Rivas-Martínez (2004) approach for vegetation thermicity, humidity and continentality thresholds.

Stand-scale environmental variables included altitude, distance to the sea, and geological background, obtained from national GIS data bases (Instituto do Ambiente, 1998; Ninyerola *et al.*, 2005). Wetland wood position within the landscape was considered important for lateral and vertical interactions. Three situations were recognized in the field: (1) fluvial backswamps where wetland woods are located at low energy, and waterlogged sub-basins with different degrees of connectivity from the main river channel; (2) littoral, when the wetland wood is associated with an endorrheic coastal lagoon; and (3) interfluvial, when the wetland wood is located on a plateau that is not obviously dependent on the surrounding hydrography (Mateus, 1999).

Within-stand geomorphic settings were summarized using wetland classifications (Semeniuk & Semeniuk, 1995, 1997; Brinson & Malvárez, 2002) of flat, basin, slope and channel main landforms. Four classes (adapted from Tiner, 1999) were defined for duration of water submersion: 1, 1 week to 1 month (winter waterlogging); 2, 1–3 months (winter submersion); 3, 3–6 months (winter-spring submersion); and 4, > 6 months (submersed during the entire growing period). Data on the duration of the submersion period and the origin of the water were obtained from the National Water Institute. Summer water level was also grouped into four classes: 1, above tree roots; 2, above herbaceous roots; 3, at ground surface; 4, above ground surface.

In order to reduce collinearity and enhance the explanatory power of environmental variables, the best were selected from the initial data set (Appendix S2), using a Monte Carlo test (999 permutations) in canonical correspondence analysis (CCA) according to a criterion of variance explained until there is no significant variable to be added to the model (ter Braak & Šmilauer, 2002). Prior to analysis, binomial variables were transformed using PC-ORD4 (McCune *et al.*, 2002), with the Beals smoothing routine – a community data-transformation technique that reduces data noise by enhancing the strongest patterns (McCune, 1994). Environmental quantitative variables were log-transformed under natural logarithms [$y = \ln(y + 1)$], and standardized by row centering (Lepš & Šmilauer, 2003) in order to make them comparable.

Data analysis

Plant community patterns

Plant community patterns were analysed in the light of both species diversity and composition. This approach made it possible to display a more precise and complete image of the wetland woods' spatial variation and, as has been highlighted in previous studies (Hérault & Honnay, 2005), reduced the dangers of relying solely on broad community measures.

Total species richness for all sites was used as an estimator of alpha diversity. In order to overcome the problem of different plot size, species richness was calculated using a fixed area of 100 m^2 for each plot. Alpha and gamma diversity were then calculated for the woods under study and for other woods in the Iberian Peninsula and Europe, with the aim of placing Ibero-Atlantic wetland wood diversity within a European frame of reference. Using the available sources of floristic data from large-scale surveys (Table 1), we applied Schluter & Ricklefs' (1993) formula for gamma diversity (= average species richness × inverse of average frequency of a species × sample size). In order to allow comparability of sampling frames, data from available studies were considered for analysis only when plot area varied less than ± 10% from that used in the present study. Tukey tests were used to elucidate alpha diversity differences between Ibero-Atlantic and other European woods.

When studying the compositional differences between woods, only trees, shrubs, non-annual herbaceous species and ligneous climbers (as per Tutin *et al.*, 1964–80) were included in the floristic matrix. This was done to reduce the effect of variability caused by particular conditions that may have prevailed during the year of sampling and been reflected by the annual species (Renöfält *et al.*, 2005).

In order to study discontinuities in floristic patterns, hierarchical clustering using the Bray–Curtis dissimilarity and group average clustering method was performed with PRIMER 5.2.9 (Clarke & Gorley, 2001). PRIMER's ANOSIM (analysis of similarities) routine was used to analyse the statistical significance of any groups that were obtained. ANOSIM permits a statistical test (one-way layout) of the null hypothesis that there are no differences in composition between groups of samples. The SIMPER (similarity percentages) routine makes it possible to identify the species that account primarily for the observed assemblage differences, revealing the indicator species for each group. The indicator species for each group and the statistical significance of differences were used to analyse the assemblage composition.

The floristic data set was also subjected to ordination procedures using CANOCO ver. 4.5 (ter Braak & Šmilauer, 2002) to explore the floristic patterns. Detrended correspondence analysis (DCA) was first used to test whether to employ a model with a unimodal response curve, or one with a linear response curve in the analysis. Only if the lengths of the ordination axes are *c.* < 2 SD will most of the response curves be monotonic, otherwise the unimodal model provides the best fit for the data (Jongman *et al.*, 1995). In the present case, we obtained gradient lengths of 3.844, 3.498 and 2.043 for the first three axes, which supported the choice of the unimodal model. The ordination was applied at two levels of division of the hierarchical classification, and we opted for DCA or correspondence analysis (CA) depending on the characteristics of the floristic data set. When CA was applied to the whole floristic matrix, a pronounced arch effect was produced between the extremes of the geographical gradient in the CA biplot (Hill & Gauch, 1980). DCA was therefore used in the analyses of all the stands (114 plots). At the second level of division of the hierarchical classification, there was no arch

Table 1 Examples of European forest ecosystems: wetland, riparian and mesic woods considered at regional and macro-scale areas of Europe, and values for alpha (average species richness 100 m^{-2}) and gamma diversity for the region surveyed, calculated following the formula (= average species richness × inverse of average frequency of a species × sample size) proposed by Schluter & Ricklefs (1993).

Community	Geographical region	Area (km^2)	Alpha diversity	Gamma diversity	Source of floristic data
Wetland woods	Atlantic coastal belt of Iberian Peninsula	75,000	23.8	2.51	This paper
	North and Central Europe	350,000	39.1	1.58	Döring-Mederake (1990)
	Baltic region	152,000	25.9	2.55	Prieditis (1997)
Riparian woods	Iberian Peninsula	600,000	50.1	3.5	Costa *et al.* (2005)
	West Iberian Peninsula (Portugal)	92,000	57.9	4.55	Aguiar *et al.* (2006)
	Central France	20,000	29.5	3.56	Botineau (1985)
Mesic woods	West Iberian Peninsula (Portugal)	60,000	22.7	4.2	Espírito-Santo *et al.* (2005)
	North Iberian Peninsula	25,000	34.6	5.0	Amigo *et al.* (1994)

effect. Therefore, and so as to avoid the destruction of ecologically meaningful information (Jongman *et al.*, 1995), we did not employ detrending techniques when using the reduced data set. Groups obtained in the classification were then superimposed onto the ordination diagram.

Multiscale drivers of plant composition

Using both the abundance data sets that had been defined by dissimilarity criteria in the hierarchical classification, we performed a constrained ordination using detrended canonical correspondence analysis (DCCA) and CCA to obtain the main explanatory variables at each scale of variation (regional, stand and within-stand) for both data sets.

Partial CCA (pCCA) was used to assess the relative contribution that each of the three sets of explanatory variables (regional, stand, within-stand) made to structuring the floristic trends. Partial CCA was thought appropriate because it allows variance partitioning between several user-defined groups of variables (two groups: Borcard *et al.*, 1992; Heikkinen & Birks, 1996; three groups: Hérault & Honnay, 2005) in order to evaluate the distribution of the explained variability across the data matrices. Seven pCCAs were completed for each component: three gave the pure regional, pure stand and pure within-stand components, and the other four represented the variation that results from the joint effect of two or three sets of variables. The total explained variation was obtained from the sum of the seven components. Each component of the variation was obtained by dividing the canonical eigenvalues of a particular CCA (or pCCA) by the total inertia – the sum of all the eigenvalues of a CA of the floristic abundance matrix.

Multiscale drivers of diversity

Linear mixed-effects models were implemented in R ver. 2.1.1. (R Development Core Team., 2004) with the *lme* function (Pinheiro & Bates, 2000) to model the relationship between regional, stand and within-stand explanatory variables and species richness. The *lme* function enabled us to include the stand × plot interaction as a random effect, accounting for the hierarchical structure of our sampling design and producing the appropriate error terms of multiscale variables in a single model. We used the methods described by Burnham & Anderson (2002), with forward stepwise variable selection based on the information-theoretic approach. This methodology has been applied recently in long-term modelling of plant richness variation (Willis *et al.*, 2007). The approach compares the fits of a suite of candidate models using the Akaike information criterion (AIC), which allows models with different numbers of parameters to be directly compared with one another. The AIC is calculated for a suite of models, and the best fitting and most parsimonious one has the smallest AIC (termed $\mathrm{AIC}_{\mathrm{min}}$). AIC differences are calculated relative to this minimum, so for model i the AIC difference (Δ_i) is calculated as: $\Delta_i = \mathrm{AIC}_i - \mathrm{AIC}_{\mathrm{min}}$.

The absolute size of the AIC is unimportant; instead, the difference in AIC values between models indicates the relative support for the models. In order to compare models, we calculated Akaike weights, w_i (cf. Burnham & Anderson, 2002):

$$w_i = \frac{\exp\left[-\left(\frac{\Delta\mathrm{AIC}_i}{2}\right)\right]}{\sum \exp\left[-\left(\frac{\Delta\mathrm{AIC}_i}{2}\right)\right]}$$

For all the models, the w_i add up to 1 and possess a probabilistic interpretation: for the set of models, w_i is the probability that model i would be selected as the best fitting model if the data were collected again under identical circumstances (Burnham & Anderson, 2002).

We used the set of selected variables (see selection procedure above) in order to reduce collinearity, and we tried all the combinations at the regional, stand and within-stand scales. Then we fitted the models for species richness with selected variables at each scale. We calculated the AIC, Δ_i and Akaike weights for all the models, in order to compare them between and within scales.

RESULTS

Plant community patterns

Based on the initial criteria of soil moisture and forest vertical structure, a total area of 688 ha of wetland woods was sampled across a surveyed area that covered 75,000 km^2 (Fig. 1). Altogether, 301 species were identified, including 30 bryophytes and 41 woody species, of which 13 were trees. Gamma diversity values were lower (mean 2.21, range 1.58–2.55) for Ibero-Atlantic and other European wetland woods than for Iberian riparian and mesic woods (mean 4.2, range 3.5–4.5; Table 1). Average values for species richness in Ibero-Atlantic wetland woods (mean 23.8 species in 100 m^{-2}, range 3–44) were significantly lower ($P = 0.02$) than they were for riparian woods (mean 48.0 species in 100 m^{-2}, range 29–58).

The hierarchical classification indicated five major floristic groups with 75% between-group dissimilarity (groups 1–5, named by dominant tree species: 1, *Betula alba* L.; 2, *Salix atrocinerea* Brot. + *Fraxinus angustifolia* Vahl; 3, *Salix atrocinerea*; 4, *Alnus glutinosa* (L.) Gaertner; 5, *Salix salviifolia* Brot.). The groups (Fig. 2) were discernible in the DCA ordination space. The first two axes of the DCA explained 16.7% (20.7% with the three axes) of total community variance, with eigenvalues of 0.457 and 0.289 (0.180 on the third axis). All the pairs of groups that were analysed as part of the ANOSIM procedure were significantly different ($P < 0.01$; Table 2), and were clearly separated ($R > 0.75$) except for 2 vs. 3 and 3 vs. 4. The groups could be distinguished by the dominant woody species composition and were apparently related to the latitudinal gradient (northern sites in group 1, southern sites in groups 2 and 5, with groups 3 and 4 located in between), as shown in Fig. 1. The members of the *S. atrocinerea* group (group 3) displayed the lowest richness (average 14 species in 100 m^{-2}, range 3–22), while the

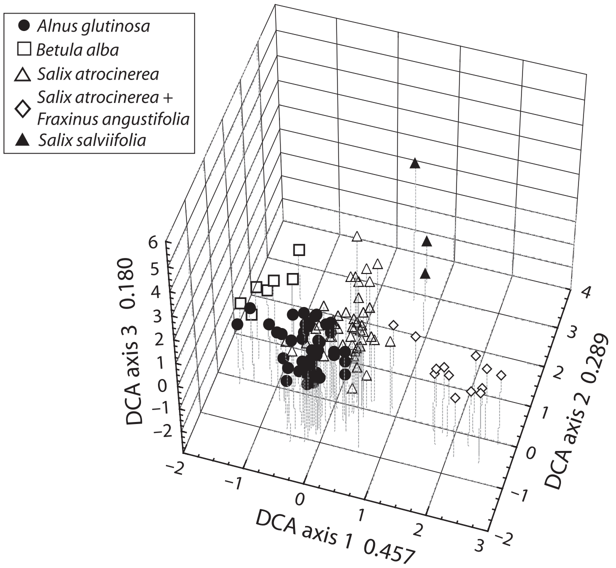


Figure 2 Detrended correspondence analysis (DCA) of perennial species (trees, shrubs, non-annual herbaceous and ligneous climbers) using all the plots. Total inertia, 4.463. Eigenvalues are indicated on axis titles. Groups obtained by hierarchical clustering (Bray–Curtis dissimilarity and group average) are superimposed and shown by different symbols (level of dissimilarity = 75%).

A. glutinosa group (group 4) displayed the most species-rich communities (average 31 species in 100 m^{-2}, range 14–44). The *B. alba* (1), *S. atrocinerea + F. angustifolia* (2) and *S. salviifolia* (5) groups showed intermediate average values: 20.3, 24.8 and 30 species in 100 m^{-2}, respectively. Ordination and hierarchical clustering showed that 86% of the stands belonged to groups 3 (*S. atrocinerea*, willow) and 4 (*A. glutinosa*, alder) as opposed to the barely represented groups 1, 2 and 5 (see Appendix S3 for the indicator species in each group). Hierarchical clustering and ordination analysis were repeated for the alder and willow groups in order to understand better the underlying floristic patterns. Classification first divided the sites into two groups with 75% dissimilarity, which were dominated by alder and willow species, respectively, and largely corresponded to the same two groups (3 and 4) as had been found in the previous analysis. The next level of dissimilarity was 62%, thus indicating a less clear separation between the eight groups created (four willow and four alder groups). The statistical significance of differences between groups (obtained using ANOSIM) indicates that groups are different, but not discrete ($0.40 < R < 0.72$). Alder was considered typical at the first level (75%) of the cluster and occurred only marginally in willow groups.

Multiscale drivers of species composition

The selection procedure for the environmental variables controlling the floristic patterns retained 20 variables that were significantly ($P < 0.05$) related to the species distribution using the Monte Carlo permutation test (Table 3). When all the sites were subjected to DCCA, the highest correlations were displayed by regional variables (potential evapotranspiration, PET; compensated thermicity index; number of sun hours per year; number of days of precipitation; air annual humidity) and by altitude with the first DCCA axis; in general axes 2 and 3 display lower correlations, except with distance from the sea and the continentality index, both on axis 3. The CCA of willow and alder woods revealed that correlations with regional variables and axis 1 decreased compared with the equivalent analysis (DCCA) with all the sites. Part of the floristic variation is explained within the second and third axes of the ordination by stand and within-stand variables. Duration of submersion and summer water level had the highest correlations with axis 3, and distance to the sea had the highest correlation with axis 2 (Table 3).

The pCCA of willow and alder woods accounted for 37.5% of the total explained variation, while 63.5% remained unexplained. Of the total explained variability, the highest proportion of variation (18.5%) corresponds to pure fine-scale variables (stand and within-stand), while 11.9% is due to pure

Table 2 Analysis of similarity of cluster groups (ANOSIM).

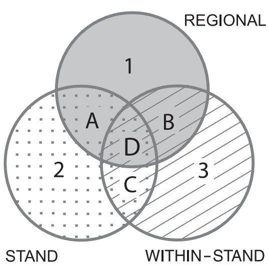
Groups by number	Groups by dominant overstorey species	*R*-statistic	*n*
1 vs. 5	*Betula alba* ⇔ *Salix salviifolia*	1.0**	11
1 vs. 2	*B. alba* ⇔ *Salix atrocinerea* + *Fraxinus angustifolia*	0.989***	21
5 vs. 2	*S. salviifolia* ⇔ *S. atrocinerea* + *F. angustifolia*	0.969**	16
4 vs. 5	*A. glutinosa* ⇔ *S. salviifolia*	0.980**	47
3 vs. 5	*S. atrocinerea* ⇔ *S. salviifolia*	0.945***	48
3 vs. 1	*S. atrocinerea* ⇔ *B. alba*	0.937***	53
4 vs. 2	*A. glutinosa* ⇔ *S. atrocinerea* + *F. angustifolia*	0.875***	57
4 vs. 1	*A. glutinosa* ⇔ *B. alba*	0.803***	52
3 vs. 2	*S. atrocinerea* ⇔ *S. atrocinerea* + *F. angustifolia*	0.609***	48
4 vs. 3	*A. glutinosa* ⇔ *S. atrocinerea*	0.555***	89

R-statistic ranges between 0 (identical) and 1 (totally dissimilar); *n*, number of cases for each *P* value calculated. $R > 0.75$, well separated groups; $R > 0.5$, overlapping but clearly different; $R < 0.25$, barely separable (Clarke & Gorley, 2001). Global *R* for all samples = 0.71***.
**$P < 0.01$; ***$P < 0.001$.

Table 3 Environmental variables retained for analysis after forward selection procedure using Monte Carlo test and correlations of canonical axes with the selected environmental variables calculated for two levels of analysis of the floristic matrix: using all woods, $n = 114$; willow and alder woods, $n = 84$.

Environmental variables		DCCA (all woods)			CCA (willow and alder woods)		
		Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
REGIONAL							
Y	Longitude	**0.41**	−0.02	0.04	−0.01	**0.23**	0.09
PET	Potential evapotranspiration	**0.75**	**0.16**	0.07	**0.55**	0.03	**−0.17**
ITC	Compensated thermicity index	**0.85**	0.10	**−0.18**	**0.43**	**0.47**	−0.15
Ic	Continentality index	**0.17**	−0.03	**0.30**	0.10	**−0.30**	0.00
Pwin6/P	Ratio winter/annual precipitation	**0.44**	**0.21**	**0.18**	**0.41**	**−0.18**	−0.01
Sun_hour	Number of sun hours year^{-1}	**0.65**	**0.29**	0.04			
P_days	Number of days of precipitation	**−0.75**	**−0.33**	−0.02			
Ann_hum	Air annual humidity	**−0.46**	**−0.26**	−0.00	**−0.35**	−0.10	0.07
STAND							
Sea_dist	Distance to sea	**−0.33**	**0.30**	**0.45**	**0.21**	**−0.48**	−0.02
Alt	Altitude	**−0.60**	0.09	0.00	**−0.23**	−0.10	**0.31**
Plain_w	Wetland width	**−0.25**	−0.09	**0.18**	**−0.18**	**−0.22**	0.07
Lands_f	Fluvial position in landscape	**0.19**	**0.20**	**0.22**	**0.20**	**−0.32**	0.06
Lands_v	Littoral position in landscape	−0.09	**−0.23**	**−0.29**	**−0.23**	**0.35**	−0.13
Lands_i	Interfluvial position in landscape	**−0.19**	−0.06	−0.04			
WITHIN-STAND							
Channel	Wetland shape: channel	**0.23**	**0.18**	0.13	−0.02	−0.07	**0.17**
Inund_s	Duration of water submersion	**0.25**	**−0.20**	**0.24**	**−0.18**	**−0.20**	**−0.53**
Summ_lev	Summer water level	**0.23**	**−0.24**	**0.16**	**−0.16**	−0.11	**−0.47**
Riv_dist	Distance to nearest river	**0.14**	−0.10	−0.04	0.04	0.07	**−0.16**
Strahler	Strahler order number of nearest river	0.08	**0.22**	0.01	0.13	**−0.21**	−0.14
Orig_fre	Phreatic origin of water	**−0.17**	−0.05	−0.05	−0.04	0.10	0.07
Eigenvalue		0.39	0.19	0.11	0.18	0.13	0.12
Cumulative percentage variance of species–environment relationship		23.1	34.7	40.8	15	26	35
Trace (%)			37.70			38.78	

Explanatory variables that were significantly related to the species distribution selected from the initial environmental matrix are shown grouped in the three scales of analysis: regional, stand and within-stand. Significant correlations at $P < 0.05$ are indicated in bold. Terms are defined in Appendix S2.



Code	Contribution to Total Variance (%)	Source of Explained Variance
1	11.9	Pure Regional
2	8.9	Pure Stand
3	9.6	Pure Within-stand
A	2.4	Shared Regional + Stand
B	1.8	Shared Regional + Within-stand
C	2.9	Shared Stand + Within-stand
D	0.0	Shared Regional + Stand + Within-stand
Σ	37.5	TOTAL EXPLAINED

Figure 3 Results of variance partitioning. Percentages of contribution of each set of selected environmental variables obtained by partial canonical correspondence analysis (pCCA) using *Salix atrocinerea* and *Alnus glutinosa* woods.

regional variables. The shared components of the variation accounted for much lower values: regional + stand, 2.4%; regional + within-stand, 1.8%; stand + within-stand, 2.9%; regional + stand + within-stand, 0% (Fig. 3).

In order to illustrate and examine the ordination results, Figs 4 and 5 show the distribution of the floristic abundances of willow and alder woods, constrained by explanatory variables that are globally considered (CCA) and shown separately at each scale of analysis (pCCA). Axes 1 and 3 are represented in both figures because these axes generally displayed the highest correlations with explanatory variables (Table 3). Consistent with the medium R values that we found using ANOSIM ($0.40 < R < 0.72$), it is possible to observe a transitional pattern rather than discrete floristic groups in both CCA and pCCA biplots. The first CCA axis (Fig. 4; abbreviations of environmental variables follow Table 3) is related to a climatic gradient (PET, Itc, Pwin6/P, Ann_hum), while the third axis is related to within-stand hydrological variables (Inund_s, Summ_lev, Riv_dist). Stand variables (Alt, Lands_v, Plain_w) reveal a gradient of variation between axes 1 and 3.

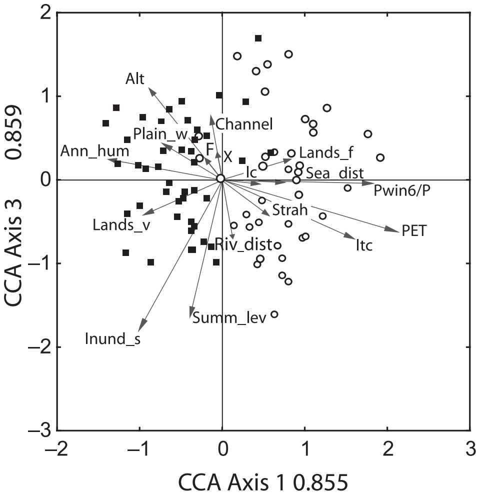


Figure 4 Canonical correspondence analysis (CCA) biplot of *Salix atrocinerea* (white circles) and *Alnus glutinosa* (black squares) woods constrained by the best explanatory environmental variables selected using Monte Carlo permutation tests. Correlations between floristic and environmental canonical axes are shown. Abbreviations of environmental variables are as in Table 3; F = phreatic origin of water.

The variation due to stand variables is actually correlated with axis 2 (Table 3). The pCCA biplots make it possible to visualize the main gradients of plant composition at each scale. The pCCA biplot representing pure regional components of variation (Fig. 5) reveals an image that is similar to that displayed in the global CCA (Fig. 4), indicating a regional effect on the abundance of willow and alder woods. The main gradients at the stand scale were given by Plain_w and Sea_dist, while Inund_s, Summ_lev, Strahler, and Riv_dist are the main within-stand gradients.

Multiscale drivers of species diversity

A summary of the best linear mixed models for species richness at each scale is given in Table 4. We present the results obtained for all the models up to 0.99 of the total Akaike weights ($\sum w_i = 1$ for all models tested) – the models that are not shown represent only < 0.1 of the probability of the best fitting model.

The best model ($\beta_0 + \beta_1 \times$ Riv_dist $+ \beta_2 \times$ Inun_s) was found at the within-stand level of variation, and represents 60% of the probability of being selected as the best fitting model if the data were to be collected again under identical circumstances (Burnham & Anderson, 2002). At the same scale, there is a second model ($\beta_0 + \beta_1 \times$ Riv_dist) that can be seen as an alternative to the selected model, as $\Delta_i < 2$ (Burnham & Anderson, 2002). All the models that were fitted for the regional-scale data had values of $\Delta_i > 10$, which means they essentially had no support. At the stand scale, the model $\beta_0 + \beta_1 \times$ Plain_w was at the limit of this benchmark. It therefore offered less support, but was not totally rejectable. Based on AIC differences (Δ_i), it seems clear that species

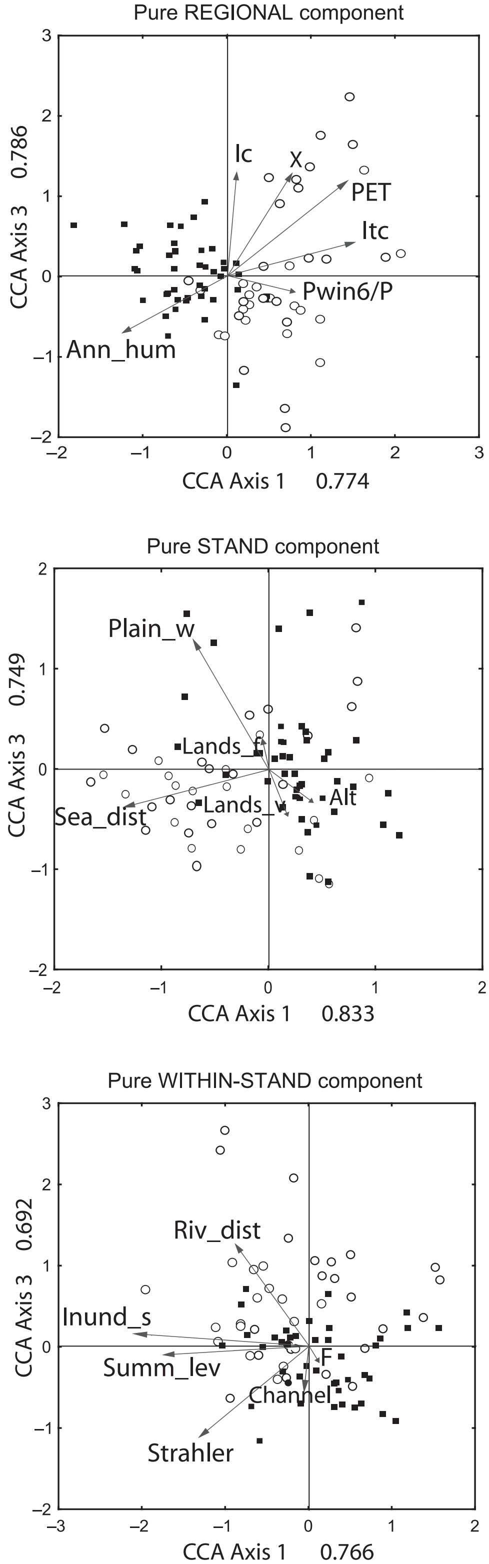


Figure 5 Partial canonical correspondence analysis (pCCA) pure components of environmental variation for each of the three scales of analysis: regional, stand and within-stand. Biplot scores represent *Salix atrocinerea* (white circles) and *Alnus glutinosa* (black squares) woods. Abbreviations of environmental variables are as in Table 3; F = phreatic origin of water. Correlations between floristic and environmental canonical axes are shown.

Table 4 Ranking of best models at each scale of variation used to explain species richness from AIC-based model selection.

Scale	Best models	Coefficients			AIC	Δ_i	w_i
		β_0(SE)	β_1(SE)	β_2(SE)			
Regional	$\beta_0 + \beta_1 \times$ Pwin6/P	11.98 (9.91)	0.18 (0.14)	–	772.33	15.63	0.00
	$\beta_0 + \beta_1 \times$ PET	7.28 (14.87)	0.02 (0.02)	–	772.59	16.00	0.00
	$\beta_0 + \beta_1 \times$ PET + $\beta_2 \times$ Pwin6/P	4.80 (15.13)	0.01 (0.02)	0.13 (0.16)	773.93	17.23	0.00
Stand	$\beta_0 + \beta_1 \times$ Plain_w	26.78 (1.26)	−0.01 (0.00)	–	766.70	10.00	0.01
	$\beta_0 + \beta_1 \times$ Plain_w + $\beta_2 \times$ Sea	25.92 (1.54)	−0.01 (0.00)	0.04 (0.04)	767.80	11.1	0.00
	$\beta_0 + \beta_1 \times$ Plain_w + $\beta_2 \times$ Lands_f	17.45 (10.20)	−0.01 (0.00)	10.40 (11.29)	767.90	11.2	0.00
Within-stand	**$\beta_0 + \beta_1 \times$ Riv_dist + $\beta_2 \times$ Inun_s**	21.61 (2.63)	−0.02 (0.00)	1.28 (0.77)	756.70	0.00	**0.60**
	$\beta_0 + \beta_1 \times$ Riv_dist	25.77 (0.92)	−0.03 (0.00)	–	757.45	0.75	0.38
	$\beta_0 + \beta_1 \times$ Inun_s	20.13 (1.32)	1.32 (0.83)	–	771.00	14.3	0.00

Δ_i = AIC differences (calculated as the difference between the AIC of each model and the AIC of the best model), w_i = Akaike weights (probability that model *i* is the actual best model of the set), SE = standard error. Only models with the lowest AIC for each scale are shown, such that the sum of weights is 0.99. The weight of the model with the greatest support, given the data, is highlighted in bold type.

Table 5 Significance of variables retained for the best models used to explain species richness at each scale of variation.

Scale	Best models	Variable					
		Name	Significance	Slope	Name	Significance	Slope
Regional	$\beta_0 + \beta_1 \times$ PET	PET	0.2567	$\beta_1 > 0$	–	–	–
	$\beta_0 + \beta_1 \times$ Pwin6/P	Pwin6/P	0.2170	$\beta_1 > 0$	–	–	–
	$\beta_0 + \beta_1 \times$ PET + $\beta_2 \times$ Pwin6/P	PET	0.5347	$\beta_1 > 0$	Pwin6/P	0.4283	$\beta_2 > 0$
Stand	$\beta_0 + \beta_1 \times$ Plain_w	Plain_w	0.0068**	$\beta_1 < 0$	–	–	–
	$\beta_0 + \beta_1 \times$ Plain_w + $\beta_2 \times$ Sea	Plain_w	0.0042**	$\beta_1 < 0$	Sea	0.3484	$\beta_2 > 0$
	$\beta_0 + \beta_1 \times$ Plain_w + $\beta_2 \times$ Lands_f	Plain_w	0.0085**	$\beta_1 < 0$	Lands_f	0.3605	$\beta_2 > 0$
Within-stand	$\beta_0 + \beta_1 \times$ Riv_dist + $\beta_2 \times$ Inun_s	Riv_dist	0.0001***	$\beta_1 < 0$	Inun_s	0.1020	$\beta_2 > 0$
	$\beta_0 + \beta_1 \times$ Riv_dist	Riv_dist	0.0001***	$\beta_1 < 0$	–	–	–
	$\beta_0 + \beta_1 \times$ Inun_s	Inun_s	0.1179	$\beta_1 > 0$	–	–	–

**$P < 0.01$; ***$P < 0.001$.

richness is conditioned mainly by finer-scale variables, namely distance to the river and water submersion.

If we analyse the significance of variables retained in the models (Table 5), we find that significant variables were found only at stand and within-stand levels of variation. Distance to the river was highly significant and displayed a negative slope, indicating a reduction in species richness at sites located far from the river course. Although less obvious, plain valley width was also significant in the models that were fitted at stand scale. These results are consistent with the AIC differences, suggesting that species richness is more a function of local variables than of regional ones, and that the relationship with the fluvial corridor within the hydrographic basin plays a fundamental role in diversity patterns.

DISCUSSION

Plant community patterns

A search of the whole Atlantic coastal belt of Iberia, a major part of which is truly Mediterranean from the biogeographical (Cox, 2001) and bioclimatic (ombrothermic indices) points of view (Rivas-Martínez, 2004), found a small (688 ha) but significant area of wetland woods (Appendix S1; Fig. 1). The Mediterranean region in general, and the Iberian Peninsula in particular, are considered to form a biodiversity hotspot (Médail & Quézel, 1999; Myers *et al.*, 2000). However, in our study, low species richness and a large number of common taxa per plot compared with mesophytic and riparian woods were found to be typical features in most stands. These values resulted in low gamma diversity along the whole Ibero-Atlantic latitudinal gradient, which is consistent with other European wetland woods (Döring-Mederake, 1990; Prieditis, 1997; Schnitzler *et al.*, 2007). Ibero-Atlantic wetland woods also displayed lower gamma diversity than Iberian mesic woods. This result suggested that the main drivers of wetland woods species variation differ from the general patterns governing terrestrial species, which are generally explicable in relation to geographical and climatic gradients.

When we studied plant composition, we found five woodland types based on tree species (Figs 1 and 2), which is consistent with some of the existing European classifications (Kelly & Iremonger, 1997; Prieditis, 1997; Rodwell, 1998). Several authors have discussed the continuous or discontinuous nature of vegetation (Mucina, 1997), and whether it is possible to classify a section of vegetation into discrete units when it is subject to continuous change (Glavac *et al.*, 1992), as is the case with wetland systems. Most of the stands belonged to alder and willow types with transitional phases between them, as reported in an earlier study on north-western Iberian wetland woods (Rodríguez-González et al., 2004). A number of authors consider willow woods to be a prior successional stage to alder woods (Haslam, 1965; Lugo, 1990; Amigo *et al.*, 2004). However, the willow community may also represent the end point of colonization by woody species in the wettest soils (Rivas-Martínez *et al.*, 1980; Kelly & Iremonger, 1997; Rodwell, 1998; Neto, 2002). Although alder and willow woods were not clearly discrete entities in terms of species abundances, willow woods were the poorest formations in terms of species richness. Willow scrub formations were also found to be the poorest in a recent meta-analysis of European floodplain forests (Schnitzler *et al.*, 2007). In north-western Iberian wetland woods, willow presence was related to high periods of soil inundation (Rodríguez-González *et al.*, 2004). Low species richness seems to be a frequent feature in forests that have developed in waterlogged soils in several regions, including tropical (López & Kursar, 2003) and temperate (Amigo *et al.*, 2004), with the boreal being the exception (Ohlson *et al.*, 1997). Several authors have referred to reductions in richness related to excessive levels of soil water and the subsequent anoxic environment (Lugo, 1990; Rheinhardt *et al.*, 1998; Whittaker *et al.*, 2001; Amigo *et al.*, 2004). Nearly all the species – even the highly tolerant ones – require an absence of flooding for seed germination (Jones & Sharitz, 1998; Casanova & Broc, 2000), and this can lead to the exclusion of a number of species when excessive soil moisture persists.

Multiscale drivers of species diversity and composition

When we analysed the scale at which environmental drivers influenced either species composition or diversity, the results were consistent: finer-scale factors were shown to play a relevant role in plant species variation for both community properties. An analysis of plant composition, which was applied at two levels of hierarchical classification dissimilarity, revealed two scales of main determinants of plant abundances. When considering the whole set of wetland woods (five floristic types), a primary regional (climatic) effect is present in the distribution of plant abundances. At the second level of hierarchical cluster dissimilarity, which represents 86% of the sites (alder and willow woods), we observed a decrease in regional importance and an increase in the correlations of ordination axes with finer-scale variables (Table 3). It is generally considered that at the macroscale, the climate water–energy gradient is the main factor governing the variation of plant species (O'Brien *et al.*, 2000; Whittaker *et al.*, 2001). For terrestrial vegetation in Europe, the main environmental drivers have been found to be regional (geographical and climatic) ones (Hill, 1991). Recent studies have demonstrated that geographical gradients in plant variation – in particular that of woody plants such as trees and shrubs – can be seen as by-products of water–energy dynamics, which is the fundamental climate-driving process (O'Brien, 2006). Our study area comprises a strong climatic gradient that is reflected in dramatic changes in terrestrial vegetation from a temperate region (north-western Iberia) to a Mediterranean one (south Iberia). Nevertheless, our results showed that stand and within-stand factors together represent a higher proportion (18.5%) of explained variation than regional (11.9%) factors. Hydrogeomorphic variables, such as duration of water submersion, summer water level, position in the landscape and distance to the river, appeared to be relevant drivers of plant composition. Significant regional effects are consistent with hypotheses that link species variation to the unique history and geography of a region, independently of local ecological conditions (Schluter & Ricklefs, 1993). Although local determinism has recently been questioned (Ricklefs, 2004), fine-scale variables have also been found to be important in community composition studies conducted in floodplain forests (Hérault & Honnay, 2005). Kroes & Brinson (2004) found that climatic variables such as potential evapotranspiration and precipitation explained only some of the factors involved in supporting wetland conditions, and that a more local presence of wetland indicators, dictated by water-table position and inundation, was responsible for the variation. Given the adverse Mediterranean climate, the prevalence of wetlands and their unique species assemblages is therefore determined more by a lack of effective drainage than by supplementary supplies of water, which are typically lacking in these geographical regions (Comerford, 1996; Brinson & Malvárez, 2002).

In terms of species richness, the analysis clearly indicated that finer-scale variables were an important influence for the whole data set. The models that were fitted with regional variables had no support in terms of AIC differences, and the best models indicated a significant negative relationship between distance to the river and species diversity. It has been the working hypothesis of floodplain ecologists that the establishment of uncommon levels of species richness on floodplains is a result of the unique processes that occur within floodplain ecosystems (Mouw & Alaback, 2003). It is also assumed that local richness on floodplains is increased by species migrating from upstream regions and colonizing the floodplains (Décamps & Tabacchi, 1994). While long-distance dispersal by wind explains relatively little variation in regional plant survival (Soons & Ozinga, 2005), on floodplains, dispersal supported by the fluvial corridor and river-related processes have been found to be the main drivers of species richness (Renöfält *et al.*, 2005). At fine scales (stand and within-stand), contemporary Ibero-Atlantic wetland woods display several (natural or anthropic) degrees of connection with the fluvial course, with the ensuing implications in terms of the potential for species dispersion throughout the hydrographic basin. Lower species richness in the most disconnected wetland woods supports this idea. Recent studies for herbaceous species reported that long-distance dispersal both within and between regions may affect species composition in target plant communities (Zobel, 2005). In the particular case of wetland woods, the propagation of many bryophytes and vascular plants is limited to clonal growth processes at the scale of centimetres and years (Økland *et al.*, 2003).

Some authors suggest that wetland woods differ from most other previously studied ecosystems with regard to the relative importance of major determinants of plant species richness, and that if historical biogeographical factors must be invoked to explain present-day patterns, then patchily distributed forest types cannot be explained by environmental factors (McCune & Allen, 1985; Økland *et al.*, 2003). A recent study in an insular environment has concluded that historical and contemporary variables may be partially correlated with one another, and therefore cannot be considered separately (Harrison *et al.*, 2006). To shed some light on these questions, and to address the variability that remained unexplained in the present study, the current set of variables should be augmented to include those related to short-term (variations over months and years) and long-term (thousands of years) temporal change. It is not clear if these systems are a perpetual succession of a wetland (Prieditis, 1997) or a step in the succession to another type of ecosystem (deciduous mesic forest; Wheeler, 1980). Given that the time span for dominance of the most shade-tolerant species is *c.* 200–1000 years (White, 1979), the short-lived tree species that dominate Ibero-Atlantic wetland woods make it difficult to demonstrate whether shade-tolerant species, which are renowned indicators of less pioneering communities, will eventually prove dominant. The ability of wetland woods to persist over thousands of years has been reported in Eastern Europe and attributed to a cyclic development of a patchily dynamic system in the landscape (Pokorný *et al.*, 2000). The general human-induced absence of these large, self-reproducing areas in the contemporary Iberian landscape calls for long-term palaeoecological studies in order to provide a temporal background and perspective for current spatial information. The importance of considering the effects of historical processes in forest communities has been highlighted in recent studies (Ricklefs *et al.*, 1999; Hérault & Honnay, 2005), and combined palaeoecological and autoecological research has proven fruitful in wetland woods in northern Europe (Brock *et al.*, 1989; Brayshay & Dinnin, 1999; Brown, 1999). The findings from long-term studies of variation in plant richness have important implications for predicting richness.

CONCLUSIONS

True wetland woods persist in Ibero-Atlantic Mediterranean areas, even in the southernmost parts of Europe. The main patterns of their communities' spatial variation diverge partially from existing climate-dependent theories of large-scale distribution of terrestrial vegetation. The climatic influence on species composition is present along the latitudinal gradient from temperate to arid regions, but for a major proportion (86%) of the stands studied, both diversity and composition were closely related to finer-scale variables – particularly hydrogeomorphic ones (local hydrology and landscape position). In a manner that is consistent with other studies, waterlogging was determinant as a factor in the reduction of diversity, and this was more evident in willow woods. Low diversity was also found to be associated with the isolation of many remnant patches of wetland woods from the water course. Given that this was a first study on Ibero-Atlantic wetland woods, and that we selected the more pristine sites, new questions arise regarding history's role in the fragmentation patterns, and whether natural or human-induced processes affect wetland-wood species variation. Although less important than in the case of other forest communities (e.g. terrestrial), the effect of climate should not be ignored, given the extreme fragility that characterizes wetland woods. In arid regions, this fragility can lead to low resilience if the climate-independent source of water ceases for either natural or human-induced reasons. Conservation measures need to take this into account, insofar as the loss of these ecosystems would be more and more irreversible at a time of increasing climate variability.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 List of wood stands including area, different landforms, canopy dominant species, number of sampling plots and geographical coordinates.

Appendix S2 Original set of environmental variables before selection procedure, classified according to type and scale of variation.

Appendix S3 Average relative abundance (%) of the best discriminating species of each group in the cluster analysis performed for all woods, calculated by SIMPER (similarity percentages) routine.

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