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Determinants of woody species richness in Scot pine and beech forests: climate, forest patch size and forest structure

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ABSTRACT

We analysed patterns of woody species richness in *Pinus sylvestris* and *Fagus sylvatica* forests in Catalonia (NE Spain) from forestry inventory databank in relation to climate and landscape structure. Both types of forests are found within the same climatic range, although they have been managed following somewhat different goals. Overall, woody species richness significantly increased when conditions get closer to the Mediterranean ones, with milder temperatures. Differences between the two types of forests arose when comparing the relationship between richness and forest patch size. Woody species richness increased in pine forests with patch size, while the opposite trend was observed in beech forests. This pattern is explained by the different behaviour of structural canopy properties, since leaf area index and canopy cover showed a steeper increase with increasing forest patch size in *Fagus* forests than in *Pinus* ones. Accordingly, richness decreased with canopy cover in *Fagus* plots, but not in *Pinus* ones. We suggest that these differences would be related to management history, which may have enhanced the preservation of beech stands in larger forest landscape units.

1. Introduction

Plant species richness variability has been reported to be statistically correlated to many variables across spatial scales from local to regional levels. Many of these studies support the assumption that both climatic and topographic factors explain a high proportion of spatial variations in species richness (Richerson and Lum, 1980; Currie and Paquin, 1987; Currie, 1991; O'Brien, 1998). Most of the resulting models include climate-based water and energy variables, such as annual precipitation and potential evapotranspiration (PET) or actual evapotranspiration (AET), as the most accurate predictors of species richness on a large scale (Wright et al., 1993; Whittaker and Field, 2000; Hawkins et al., 2003). However, climatic variables alone are not sufficient when applied to local-scale richness.

In forest ecosystems, other factors related with the stand structural properties, such as habitat diversity (i.e. forest structure, soil heterogeneity, topography), disturbance regimes and human management often become more relevant in small-scale study areas. Thus, for a given area, a higher topographic complexity may support higher understorey species

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diversity (Iida and Nakashizuka, 1995; Yadav and Gupta, 2006). Several studies also demonstrated that loss of species richness is related to a higher level of disturbances, particularly in smaller patches (Iida and Nakashizuka, 1995; Benítez-Malvido and Martínez-Ramos, 2003; Zhu et al., 2004). The composition of understorey species is also expected to be influenced directly by forest structural properties (diametrical class distribution, leaf area index—LAI, basal area and canopy cover) (Hardle et al., 2003), that are clearly determined by forest management practices (Laatsch and Anderson, 2000; du Toit and Dovey, 2005). Particularly, the characteristics of the dominant species in the canopy (such as height, branching pattern or leaf area index) may influence understorey composition by controlling the radiation arriving to the ground, or soil characteristics (such as litter load, structure and chemical composition). In addition, the species richness at stand level may also be related to the size of forest patches which may determine the available species pool (Ricklefs, 1987), or because it reflects disturbance and management history.

A way to discriminate the effects of regional climatic variability and local structural characteristics on species richness is to compare contrasting forest types, determined by their dominant species, that are found within the same climatic range. A few studies have analysed how dominant species may influence patterns of species richness in forests. Plots situated in oak (*Quercus* spp.), pine (*Pinus* spp.) and oak-hickory (*Carya* spp.) stands had a significantly greater number of tree species than those in loblolly (*Pinus taeda*)-shortleaf (*Pinus echinata*) pine forests in southeastern USA (Stapanian and Cassell, 1999). Aspen (*Populus* spp) and jack pine (*Pinus banksiana*) stands are richer in vascular species than black spruce (*Picea mariana*) stands in Minnesota (Reich et al., 2001), and plant species richness is greater in coniferous plantations than in broadleaved secondary forests in Japan (Nagaike, 2002). These differences may be due to different habitat characteristics (fertility, soil, moisture); to functional features provided by the dominant species, which influence the resource availability (Reich et al., 2001); to differences in past management practices, or to the levels of other anthropogenic disturbances (Stapanian and Cassell, 1999; Nagaike, 2002).

Here we focus our study on comparing the patterns of woody species richness in two types of temperate forests occurring in Catalonia (NE Spain; 0°15′ E to 3°15′ E longitude, 40°30′ N to 42°40′ N latitude): *Pinus sylvestris* evergreen forests (pine, hereafter) and deciduous *Fagus sylvatica* (beech, hereafter) forests. Both species are widely distributed throughout North and Central Europe, with their southern limit in the Iberian Peninsula and Italy. In Catalonia, both species share a part of their range in mid-mountain altitudes (from approx. 600 to 1800 m a.s.l.), with similar climatic conditions (mean annual temperature between 7.4 °C and 14.6 °C and mean annual precipitations between 600 and 1400 mm). As a result of the structural and functional differences related with leaf habit, these two types of forests show contrasting differences in canopy cover and LAI (being these values around twice in beech than in pine forests), while having similar mean basal area values (Gracia et al., 2004). They have also experienced different logging history and the average size of forest patches with beech stands tends to be smaller than the average size of forest patches with pine stands.

We hypothesise that differences on woody plant richness emerge across climatic gradients and between different forest types found in this gradient, as a result of their contrasting structural characteristics. Since these characteristics are also related to processes occurring at landscape level (fragmentation, forest exploitation), stand richness would also be differently related to forest patch size in each forest type. We use mean annual temperature and the Thornthwaite aridity index (Thornthwaite index, hereafter) as variables that synthesises climatic conditions, and LAI, forest canopy and tree stem diameter distributions as variables describing major functional and structural features of forest stands. We focused on woody species richness, because that is the only information provided by the Third National Forest Inventory of Spain (IFN3), which is an extensive database on the forests in the region, including records of the occurrence of trees and shrubs.

2. Materials and methods

2.1. Study site and species

The study area is located in central Catalonia (NE of Spain). This is mainly a forested area, with dense forests occupying 63% of the total surface area of approx. 4000 km^2. We also find shrublands, grasslands in the upper altitudes and croplands, as well as urban areas (Gracia et al., 2000, 2001).

Pine forests are considered primary or secondary forests (from degradation of oak forests) (Folch, 1981) found in mountains, from 400 to 2000 m a.s.l. They are widely exploited in the region and constitute the first timber species (Terradas and Rodà, 2004). They mostly regenerate from seeds and constitute even-aged stands managed by the shelterwood system or uneven-aged stands after selective felling or natural gap dynamics (Centre de la Propietat Forestal, 1992, 1994).

Beech forests are considered primary forests occurring in humid mountain areas, from 600 to 1800 m a.s.l. (Folch, 1981). They were probably overexploited in the past (Terradas and Rodà, 2004), but they are currently recovering. The selection logging is the more common treatment applied to beech forests in the study area (Centre de la Propietat Forestal, 1992, 1994; Meson and Montoya, 1993), and it is compatible with the aesthetical, landscape and leisure values given to beech forests nowadays. Stand regeneration naturally occurs from stump sprouts or seedling establishment mostly occurring in gaps of the forest canopy. Saplings may remain for many years in the understorey until clearing. Management practices, along with the human occupation of the lowlands, greatly influence the current distribution of both forest types.

2.2. Data set

The forestry data are based on the Third National Forest Inventory of Spain (IFN3) (Ministerio de Medio Ambiente, 1997) which, in Catalonia, was carried out in 2000 and 2001. Our study data consists of 2230 circular vegetation field plots distributed in woody areas, at a rate of one plot per km^2.

The IFN3 database includes exhaustive information about trees (in circular plots normally within a 15-m radius, but they can be smaller or larger, depending on the plot's largest tree size), as well as details of the understorey (shrub and regenerative species present within a 10-m and 5-m radius, respectively). Structural variables, such as tree diametrical class distribution, leaf area index, or basal area, were taken from the inventory, and were obtained from field data combining sampling and allometric regressions. Canopy cover was visually estimated as the percentage of the canopy projection on the ground. Woody species richness was also recorded, and a classification was made of the sample plots according to the dominant tree species (defined as the species that represents more than 50% of the plot's basal area).

Among the different forest types found in the study area, we focused on the plots dominated by *Pinus sylvestris* ($N = 785$, the most frequent type) and the plots dominated by *Fagus sylvatica* ($N = 153$). Nevertheless, and to avoid bias, we only selected *Pinus* and *Fagus* plots of the same size (15 m radius, which is the most common size in the inventory) and sited in the same territory, where a gradient of humidity can be established (Thornthwaite aridity index from 40 to 120). In this way, 282 plots (211 dominated by *Pinus*, and 71 dominated by *Fagus*) were included in the study.

Two climate variables were included in the analysis: Thornthwaite aridity index and mean annual temperature. The Thornthwaite aridity index is a variable that synthesizes conditions of climatic water balance in the plots. It has been calculated by using estimates of precipitation, solar radiation and temperature from the Catalonia Climatic Atlas (Pons, 1996; Ninyerola et al., 2000), according to the formula:

$$\text{Thornthwaite Index} = (\text{Total annual precipitation} - \text{PET}) \times 100/\text{PET}$$

where PET (Potential Evapotranspiration) is calculated by the mean monthly mean temperatures and a coefficient estimated by the numbers of days in a month and the daily hours of sun as a function of latitude (Thornthwaite, 1948). The climatic values provided by The Catalonia Climatic Atlas provide mean climatic values in a collection of digital raster maps with a 180 m resolution. They were obtained from extrapolation procedures from the available climatic station network with series of at least 20 years of data for precipitation and temperature and 4 years for solar radiation. Although this index is correlated to temperature ($r = -0.65$ for mean annual temperature, $p < 0.0001$), we included mean annual temperature (temperature, hereafter) in the analysis to distinguish the effects of temperature and water balance. Temperature values were also obtained from the Catalonia Climatic Atlas.

For each plot, the forest patch sizes were obtained from the ''Mapa de Cobertes de sòl de Catalunya 1993'' (DARP, 1998), after overlaying the field plots from the IFN3, using MiraMon GIS software (Pons, 2000). While *Pinus* plots are found in a large range of forest patch sizes (between 7 and 150,000 ha), *Fagus* plots are only found in forest areas ranging from 3200 to 150,000 ha. Thus, only patches larger than 3200 ha including both *Pinus* and *Fagus* forests ($n = 7$) were included in the analysis performed to compare the effects of patch size on woody species richness of the two types of forests.

2.3. Statistical analysis

The effect of climate (temperature and Thorntwaite index) and forest type (*Pinus* or *Fagus*) on woody species richness and the interactions between climate factors and forest type were evaluated by a General Linear Model (GLM). However, as the number of woody species found in neighbouring plots may not be independent due to a spatial autocorrelation, we also performed a Mantel-test with the PASSAGE package (Rosenberg, 2002) by creating a ''geographic distance matrix'' from the Euclidean distance between the plots. Since a significant spatial autocorrelation was observed, we performed Partial Mantel tests (Fortin, 1999) for the variables included in the GLM, keeping the effect of geographical distance constant, i.e., differences on richness between pairs are correlated to differences between climate (temperature, Thornthwaite index) when the effects of spatial location are kept constant. The statistics resulting from this test are regression coefficients ($b_{AB.C}$), corresponding to the partial linear correlation of two distance matrices (A, B) after controlling for the linear effect of a third matrix (C). In our case, we used geographical Euclidean distance matrix as the ''C'' matrix, the absolute difference distance matrices of the dependant variable (woody species richness) as ''A'' matrices and each of the three independent variables (temperature, Thornthwaite index and forest type) as ''B'' matrices. Significant differences from zero in the regression coefficients were assessed by comparing with reference distributions obtained after 999 iterations that permuted the arrangement of the elements of one of the distance matrices.

We evaluated the relationship between forest patch size and woody species richness for the two types of forests. We took the 7 forest patches that include both types of forest as the study units. Accordingly, we performed a repeated measures ANOVA with the mean richness of the *Pinus* and *Fagus* plots belonging to the same patch as a dependent variable, the area of the forest patch as a between-subject factor (after log-scaling to allow normalisation) and the forest type as a within-subject factor. We also calculated the interaction between forest type and forest patch size. For the two types of forests, we analysed by regressions the relationship between the structural variables mean LAI, mean canopy cover and mean percentage of basal area of the plots found in each forest patch with the respective patch size. We also performed regressions between these variables and the respective plot richness. For the two forest types a chi-squared test was used to reveal differences in the tree stem diameter class distribution in small ($<8 \times 10^3$ ha), medium (8×10^3–5×10^4 ha), and large patches ($>5 \times 10^4$ ha). The trees found in plots belonging to the same patch size class (23, 102 and 38 *Pinus* plots, and 7, 14 and 51 *Fagus* plots in small, medium and large patches, respectively) were pooled together into the respective stem diameter class.

3. Results

According to the GLM ($r^2 = 0.295$, $F = 23.15$, $p < 0.001$), climate was a major determinant of woody species richness, since it increased with higher values of temperature, that is, as we get closer to Mediterranean conditions (Fig. 1, parameter estimate: 0.117, SE: 0.028; Table 1). Thornthwaite index did not show significant effect on species richness. Forest type failed to significantly explain woody species richness (Table 1), despite *Pinus* forests showed higher values (mean = 11.03, SD = 3.77) than *Fagus* ones (mean = 8.93, SD = 3.51). No significant interactions between the type of forest and the climate variables were observed (Table 1). A very low but significant spatial autocorrelation of richness between the plots was observed by performing a Mantel Test ($r = 0.0789$; $p = 0.004$). So, Partial Mantel Tests were carried out in order to keep the spatial factor constant. The results of the Partial Mantel correlations did not substantially change the pattern observed with GLM: temperature and Thornthwaite index analysed separately were significantly related to woody species richness ($b = 0.168$, $p < 0.001$; $b = 0.137$, $p < 0.001$, respectively), but the forest dominant species was not ($b = 0.010$, $p = 0.703$).

However, when considering forest patch size in the analysis, woody species richness increased in larger patches of *Pinus* forest, while the opposite was found in *Fagus* forest (repeated measures ANOVA, Forest type × Forest patch size interaction $F = 14.47$ $p = 0.013$). Overall, in these patches, species richness was significantly lower in *Fagus* than in *Pinus* forests ($F = 11.29$, $p = 0.020$). Forest structure variables also showed different behaviour in the two forest types, in relation to the patch area. Leaf area index (LAI) slightly increased with patch size for both forests types, but this increase was steeper in *Fagus* ($r = 0.85$, $p = 0.016$, slope = 1.17) than in *Pinus* forests ($r = 0.84$, $p = 0.019$, slope = 0.24) (Fig. 2, left). In addition, the overall canopy in *Fagus* forests became denser in larger patch sizes ($r = 0.78$, $p = 0.039$, slope = 51.85) (Fig. 2, right), suggesting a limitation for the coexistence of other canopy and understorey species. No significant relationship between canopy cover and patch size was found in *Pinus* forests ($r = 0.40$, $p = 0.378$). Accordingly, in *Fagus* plots, woody species richness was significantly lower with increasing canopy cover and this relationship was only marginally significant with LAI and

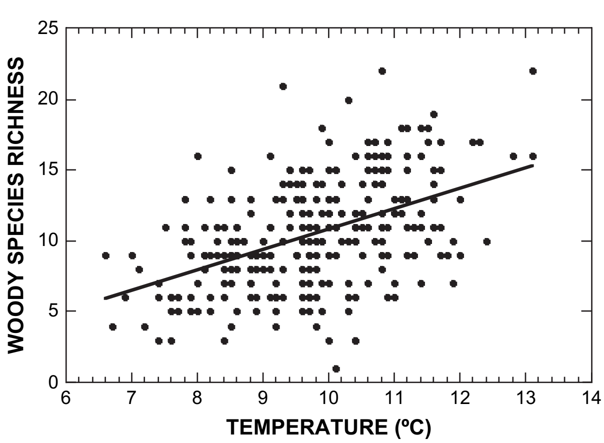

Fig. 1 – Relationship between mean annual temperature and woody species richness ($r = 0.473$, $p < 0.001$) in forest plots dominated by *Pinus sylvestris* and *Fagus sylvatica* from Catalonia (Spain) after the Third National Forest Inventory of Spain.

Table 1 – Statistical results of the relationship between woody species richness and (A) climate and forest type (GLM including for the whole set of plots); (B) forest structural variables (regressions for Fagus and Pinus plots separately)

	SS	df	*F*	*p*
(A) Climate and forest type				
Temperature	186.79	1	17.95	<0.001
Thornthwaite index	11.71	1	1.12	0.290
Forest type	2.81	1	0.27	0.604
Temperature * Forest type	8.21	1	0.79	0.375
Thornthwaite * Forest type	1.88	1	0.18	0.671
Error (Residual)	2872.00	276		
Whole model	1204.50	5	23.15	<0.001
(B) Forest structural variables	Slope	*r*	*p*	
Fagus sylvatica				
Canopy cover	−0.02	0.24	0.046	
LAI	−0.57	0.20	0.088	
Percentage of basal area	−0.05	0.21	0.081	
Pinus sylvestris				
Canopy cover	0.01	0.06	0.405	
LAI	0.78	0.11	0.136	
Percentage of basal area	−0.03	0.11	0.155	

percentage of *Fagus* basal area (Table 1). No significant relationship was found for these variables in *Pinus* plots. The percentage in basal area occupied by *Fagus* increased from 55% to 85% as the patch grows, while in *Pinus* the value decreased from 95% to 85%, although the respective correlation coefficients were not statistically significant ($r = 0.62$, $p = 0.141$, and $r = 0.72$, $p = 0.069$, respectively). Stem diameter class distribution showed significant differences between small, medium and large patches both in *Pinus* and *Fagus* forests ($\chi^2 = 44.489$, $p < 0.001$ and $\chi^2 = 21.109$, $p = 0.001$, respectively). The pattern was similar for both forest types: larger diametrical classes were more abundant in smaller patches, and they were less common in larger patches (Fig. 3).

4. Discussion

There is a general agreement about the role of energy and resource availability in explaining global patterns of decreasing forest diversity from the tropics to the poles (Wright et al., 1993; O'Brien, 1998; Whittaker and Field, 2000; Hawkins et al., 2003). Within the climatic range considered in this study, this would correspond to locations with higher temperatures, that are also closer to the Mediterranean conditions, which are well known for providing high-diversity hotspots (Quézel, 1985) and presumably also larger species pools (Ricklefs, 1987). Although Thornthwaite index was also negatively correlated to richness, this parameter failed to show significant effect in the whole model, probably as a consequence of its negative correlation to temperature. Higher values of the Thornthwaite index corresponded to colder conditions (north-facing slopes, higher altitudes) with shorter growth periods and lower energy input into the ecosystem. Neglecting the spatial autocorrelation between sampling areas can lead to erroneous results (Cliff and Ord, 1981). We successfully

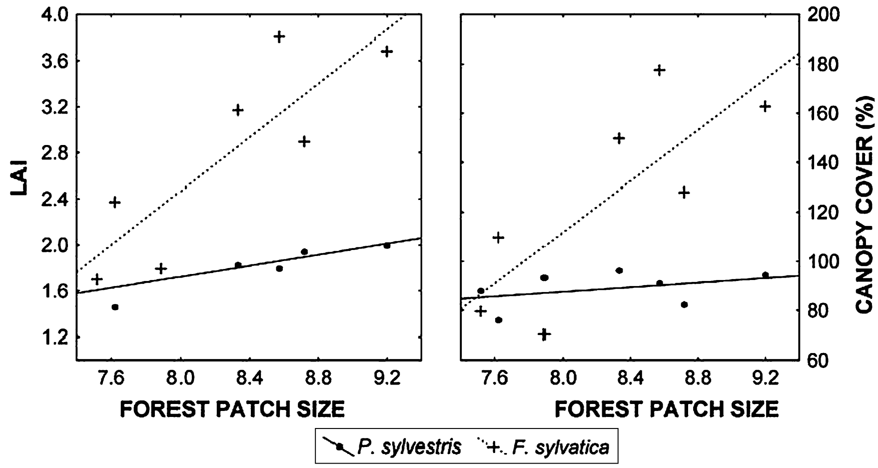

Fig. 2 – Relationship between forest patch size (log m^2) and leaf area index (left) and canopy cover (%) (right) for forests dominated by *Pinus sylvestris* and *Fagus sylvatica* from Catalonia (Spain) after the Third National Forest Inventory of Spain.

incorporated this effect, revealing a consistent pattern of decreasing richness in stands with a higher temperature.

Although pine forests stands on average showed higher woody species richness than beech ones, these differences did not achieve statistical significance. However, when including forest patch size, important differences arose between the two types of forests. While richness increased with patch area in *Pinus* plots, it decreased in plots dominated by *Fagus*. Since the distance between the plots and the limits of the forest patch (less than 200 m in 90% of cases) followed a similar pattern in both types of forest, we do not expect that differences on edge effects between the two types of forest would explain these trends. Other differences between *Pinus* and *Fagus* forests associated with topoclimatic conditions were minimised by the paired design (comparisons of *Pinus* and *Fagus* plots located within the same forest patch). Also, we analysed the occurrence of both types of forests within their common range of distribution.

However, the two types of forests differed in the relationship between some structural and functional properties and forest patch size. LAI and canopy cover increased more with patch size in *Fagus* than in *Pinus* forests. This canopy structure would explain the lower species richness in beech forest on large patches, due to light competition, as supported by the observed negative relationship between canopy cover and woody species richness. Our study was limited to woody

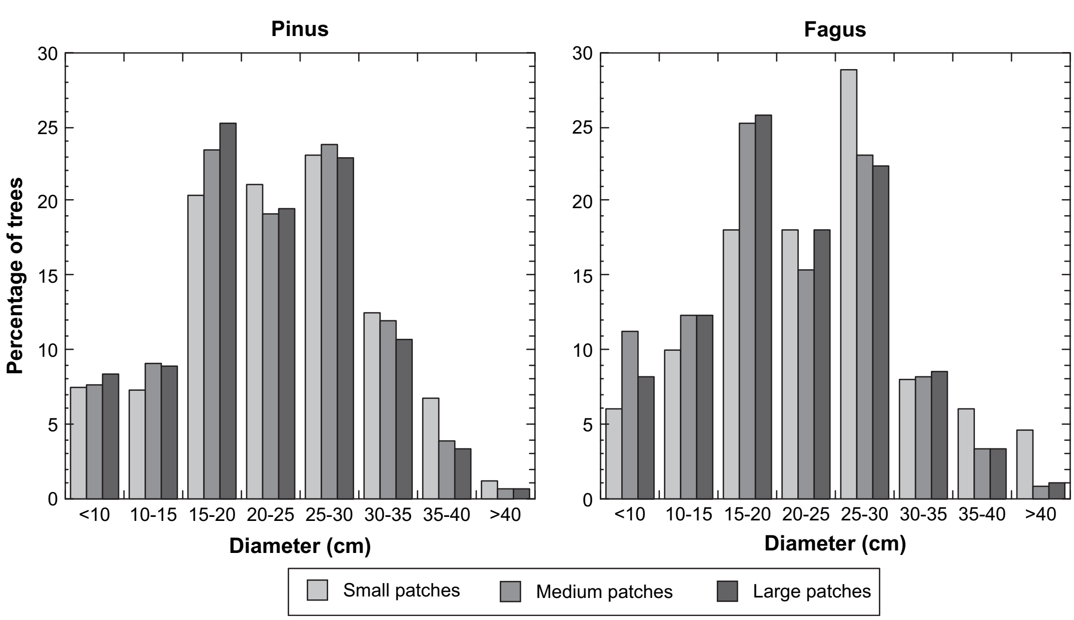

Fig. 3 – Distribution of tree stem diameter classes in *Pinus sylvestris* and *Fagus sylvatica* stands located in small ($<8 \times 10^3$ ha), medium (8×10^3–5×10^4 ha), and large forest patches ($>5 \times 10^4$ ha) from Catalonia (Spain) after the Third National Forest Inventory of Spain. Data are shown as the percentage of trees belonging to each class, after pooling all trees surveyed in plots located in the respective forest patch size class.

species since the available data bank did not include herbaceous species. However, when considering the whole set of plant species (including herbaceous ones), different patterns of relationship between canopy closure and understorey diversity may occur, as reported in temperate forests. Although a negative relationship has been shown by Balandier et al. (2002), it may shift to no effect in deciduous forests depending on moisture conditions (Hardle et al., 2003). Positive relationships may appear when open canopies favour the development of dominant woody species (i.e. *Rubus* spp.) which competitively exclude most herbs (Decocq et al., 2004). Our results support the hypothesis of overstorey control of understorey diversity through controlling light availability.

The differences in the structural properties of the canopy in relation to patch size may be related with management practices. Although both pine and beech forests are currently exploited in the region, there is a general agreement of local managers to preserve beech forests due to their chorological peculiarities. As a result, most *Fagus* plots (70.4%) are located in areas with some kind of protection status, while this only applies to 34.1% of *Pinus* plots. Also, beech stands in small isolated patches may have experienced greater human impact than in larger ones, as suggested by their lower percentage of beech basal area and more open canopies. This pattern would be different in pine forests, where the percentage of basal area decreased with patch size, and LAI only slightly increased. These practices, however, do not seem to have produced differences in the pattern of tree stem size distribution of the *Pinus* and *Fagus* stands in relation to forest patch size. In both types of forests, smaller patches support a higher proportion of larger diametrical classes. Therefore, the contribution of small trees to the increase of the percentage of basal area in large forest patches would be greater in *Fagus* stands than in *Pinus* ones.

5. Conclusion

In summary, we conclude that the climate–richness relationship is significant in Southern European forests. More specifically, warmer temperatures, associated with the neighbouring Mediterranean region, enhanced species diversity at stand level. However, stand richness patterns were also influenced by the spatial context, and particularly by forest patch size. In our case, this parameter had a different relationship with richness in beech and pine forests. Differences in canopy structure related to canopy closure, that are likely to be determined by management practices, appeared to be a reliable ultimate cause of the spatial woody species richness patterns found on a local and regional scale.

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