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The Effect of Past Forestry Activity on Mediterranean Sessile Oak Forests on the NE Iberian Peninsula

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ABSTRACT: While the sessile oak (*Quercus petraea*) may be widely distributed across Europe, it is somewhat rare on the NE Iberian Peninsula, its southern distribution and xeric limit. Understanding the relationship this forest has with not only climate factors but also with past human activity is important. This study aims to analyze the species composition and structure of sessile oak forests that form the xeric limit populations as well as examine the effect environmental factors have on them. The work was focused on the southernmost sessile oak forest, the Montseny Massif populations, which have a marked environmental Mediterranean influence. The sessile oak forest types were defined from field inventories and a cluster analysis classified the inventoried stands into five forest types. The compositional differences among the forest types were the result of past land uses and the intensity of forestry activity 50 y ago. Furthermore, the species composition is influenced by environmental factors, because more hydric stress promotes Mediterranean species. The study concludes that sessile oak are recovering from past forestry activity.

Index terms: community ecology, land use change, Montseny, *Quercus petraea*, xeric limit

INTRODUCTION

Sessile oak (*Quercus petraea* (Matt.) Liebl.) is widely distributed across Europe and, since ancient times, has been used for many purposes. For instance, its wood was used for fuel, the acorns for livestock feed, the bark for tanning, and its timber milled for construction (Eaton et al. 2016). In fact, forest ecosystems are highly exploited (Laurance et al. 2010) and the sessile oak is one of the most economically important deciduous trees in Europe (Praciak et al. 2013). Consequently, such forestry activity in Europe has generated many changes in the forest ecosystems themselves (Parviainen 2000), such as a scarcity of mature forests (Forest Europe 2015) or the presence of invasive trees coming from plantations (Krumm and Vítková 2016).

Consequently, the human activity that once took place within these forests and the resulting impact can still influence present-day forest dynamics and structure. In the Mediterranean regions in Europe, the forest was used extensively in traditional agroforestry practices but during the second half of the 20th century these practices were abandoned. As a consequence, meadows and croplands have been replaced by shrub and forest cover (UNEP 1989; Ales et al. 1992; García-Ruiz et al. 1996; Debussche et al. 1999; MacDonald et al. 2000; Santos 2000; Bou Manobens et al. 2015a) and the forest itself has grown much denser (Lasanta-Martinez et al. 2005; Améztegui et al. 2010).

Furthermore, forest dynamics are also susceptible to the effects of climate change,

which may trigger a loss of genetic diversity (Borovics and Mátyás 2013), reduce resilience (Huntingford et al. 2013; Tielbörger et al. 2014), cause forest dieback (Allen et al. 2010; Choat et al. 2012), and force species to migrate to higher altitudes (Peñuelas and Boada 2003) or shift northward (Lenoir 2008). Moreover, changes in species composition have also been reported in Europe (Reif et al. 2017). Studies show that vulnerability to climate change is different for each species (Vayreda et al. 2013). For instance, deciduous forests will experience numerous negative effects, whereas evergreen forests will not suffer quite as much (Aranda and Pardos 2000; Fotelli et al. 2009; Bou et al. 2015a).

An excellent case study of sessile oak forest dynamics can be derived from the xeric limit populations (i.e., the line between life and death for this species). Research should focus on how forest ecosystems respond to extreme environments in order to better understand xeric limit dynamics and shifts (Mátyás 2010). Sessile oak is at its southernmost xeric limit in the NE Iberian Peninsula and grows only in the cooler and moister montane forests in the region: the Pyrenees, the Guilleries, the Montnegre, and the Montseny Massif (Bou et al. 2016). With its dry summer months, the Mediterranean climate curtails sessile oak development on the lowlands. The Montseny Massif population lies within this xeric limit area and both human activity and environmental factors have changed the forest over time. The dynamics of the Montseny Massif are quite similar to the remainder of the Mediterranean region, as it too was exploited in earlier centuries. In

the Middle Ages timber was milled from the NE Iberian Peninsula oak and used in naval construction (Illa et al. 2011). However, human activity did not stop at simply harvesting the forest—people also converted natural forests into chestnut plantations (Llobet 1947; Panadera and Nuet 1986). These and other traditional forest activities were abandoned in the second half of the 20th century (Boada 2002). However, in the Guillerics-Montseny region, other more modern forest activities resulted in the abandoned chestnut plantations being replaced with stands of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Broncano et al. 2005; Ribot Porta 2016). Against this historical backdrop of human disturbance, and because of concern for the conservation of the natural heritage of the Montseny Massif (Boada 1994), the

Montseny Natural Park was established in 1977 and designated a UNESCO Biosphere Reserve in 1978 (Diputació de Barcelona 2008). The region's forests are now being affected by climate change in the form of the recent summer droughts, with some species being more vulnerable than others (Jump et al. 2006; Vayreda et al. 2013).

Sessile oak forest dynamics in the xeric limit is an important matter to investigate if the forest is to be conserved. It is to be expected that the forestry activity of the past has had and continues to have a substantial impact on forest dynamics in the NE Iberian Peninsula; however, the lack of information about the forest, its dynamics, structure, and composition make it difficult to manage and conserve. Therefore, the aim of this study was to first characterize the

sessile oak forest, and then determine the current situation in the Montseny Massif (NE Iberian Peninsula) in order to be able to protect and preserve it.

METHODS

Study Area and Sites

This work focuses on the sessile oak forest of the Montseny Natural Park (Figure 1), which represents the xeric limit of this species on the NE Iberian Peninsula. Although there are other populations along the Iberian Peninsula (e.g., the Cantabrian or Pyrenean populations), in Montseny the Mediterranean climate (Panareda 1979) has a profound influence on the oak population. The sessile oak forests in the Montseny

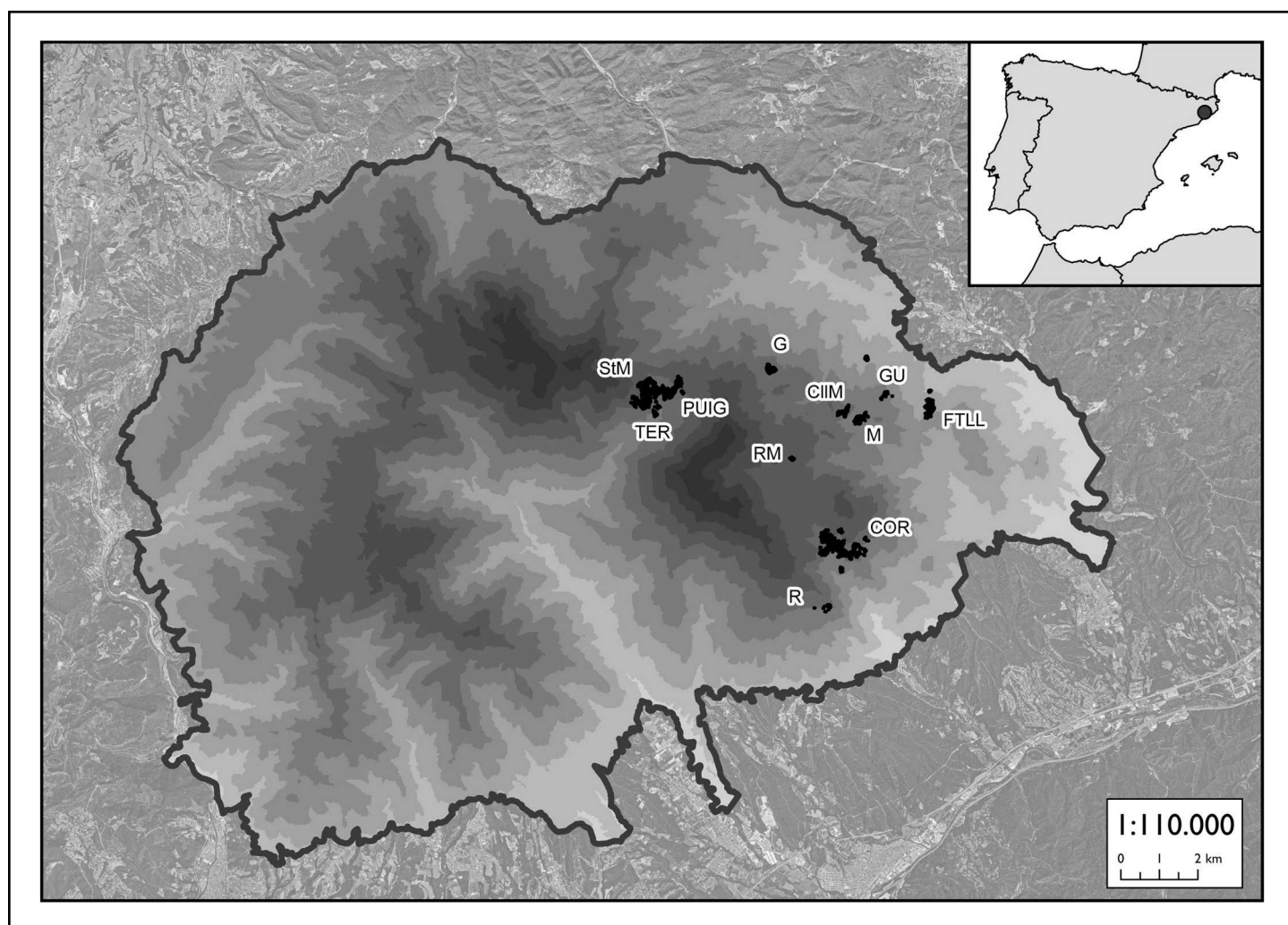


Figure 1. Sessile oak forests in Montseny Natural Park, NE Iberian Peninsula (Bou et al. 2015b). In black: all the sessile oak forest cover, with its locality labels (codes are described in Table S1).

massif cover a mere 64 ha. They are dominated by *Q. petraea* distributed into three large groups, and fragmentation of remaining stands is a problem. The sessile oak forest in the Montseny occurs from an altitude of 450–1150 m and is distributed in a narrow strip squeezed between evergreen holm oaks at lower elevations and beech at higher elevations (Bou and Vilar 2018). Granite substrate is the optimal growing condition for the sessile oak forest (Boldòs 1983), but it also can be found growing on porphyric, phyllite, and cornubite (Bou and Vilar 2018).

The climate data from the stands was estimated using specific georeferenced models of the NE Iberian Peninsula (Pons 1996; Ninyerola et al. 2000). The mean annual temperature of the study area is 10.76 °C, with a mean annual minimum temperature of 6.11 °C and a mean maximum of 15.46 °C. Annual precipitation ranges from 846.5 to 1022.6 mm.

In the NE Iberian Peninsula there are two controversial subspecies of *Q. petraea*, the more abundant *Q. petraea* subsp. *petraea* and *Q. petraea* subsp. *huguetiana* Franco & G. López. In this study, we consider *Q. petraea* in the broad sense, including both subspecies.

Stand Structural Attributes

The sessile oak forest was inventoried in 67 plots distributed over the 12 sites in the Montseny massif. Sites were systematically selected to include the main areas of the sessile oak forest habitat. The number of plots was proportional to the sample area, and plots were randomly placed to analyze the structure of the stands. At each sample location, we established a 10-m radius circular plot, in which we recorded the species name and diameter of all adult trees (individuals with a dbh >5 cm) at breast height (1.37 m). These data were then used to calculate the forest variables: density (adult trees ha⁻¹), basal area (m² ha⁻¹), mean and maximum diameter (cm), and mortality of *Q. petraea* (%). In each plot, we used 1-m² subplots to inventory *Q. petraea* regeneration, counting the number of individuals less than 1.5-m tall. We used

four subplots when we had a high density of seedlings or 16 subplots when there was a low density of seedlings. We also noted whether or not the stands had been exploited during the first half of the 20th century. To do this we used an earlier study (Bou and Vilar 2018), in which sessile oak forest was classified in different vegetation units, based on the recognizable physiognomy in the georeferenced aerial photographs taken in 1956. The exploited forests of this period were mapped and defined as “Sparse forest” and the unexploited forest as “Dense forest.”

We excluded any recently exploited forests from the inventoried stands, given that their composition had been substantially altered by the activity. For instance, one locality had a very low density of trees (477.7 stem ha⁻¹) because of forest logging 1–2 y earlier. Another example was in a locality where there was a highly anomalous composition with planted *Pinus pinaster* Aiton, the invasive *Robinia pseudoacacia* L. and a high density of fast-growing trees like *Populus tremula* L. (Bou et al. 2015b). The 58 selected samples of sessile oak stands (nota bene: from here on, understood as sessile oak stands in the general sense) are mostly located at altitudes ranging from 549 to 1178 m a.s.l. (mean 930.35 m), with gentle slopes ranging from almost flat to 30%. Aspects varied, but most stands (54%) were on south-facing slopes.

Statistical Analysis

We classified the 58 inventoried stands (Table S1) into five forest types, selecting at the 55% similarity level, using basal area data and complete linkage hierarchical cluster analysis with the Bray–Curtis similarity coefficient (the data were square-root transformed prior to analysis) for each species. The basal area of the different tree species was used as an abundance parameter to classify the different types of sessile oak forest depending on their species compositions (Table 1). The basal area is the variable that better represented abundance because all the species are well represented, and there are no problems with crowns and stature. To avoid the influence of rare species, we excluded those which

were only present in one stand (i.e., *Pyrus malus* L., *Abies alba* Mill., and *P. menziesii*). Statistical analyses were performed using Primer 6.1.11 software (Clarke and Gorley 2006) and the R environment software (R Core Team 2015).

Among the sessile oak groups obtained from the cluster analysis, the differences in the forest variables (dbh, density, basal area, diametric classes, cover, regeneration, richness, and other *Q. petraea* parameters) were analyzed using one-way ANOVA. Also, to determine the specific differences of forest types, a Tukey’s HSD was performed. To detect possible association patterns in species composition and environmental data (meteorological and topographical), we fitted the vectors of the environmental variables into a nonparametric multidimensional scaling (NMDS), and statistical significance was evaluated by 999 random permutations, using the `envfit` function of the `vegan` package in R (Oksanen et al. 2016). The environmental data used were precipitation, solar radiation, altitude, aspect, slope, and temperature (mean, minimum, and maximum). We used all the available variables, because there were not a lot and `envfit` can deal with all of them.

RESULTS

Characterization of Forest Stands

The Montseny sessile oak forest density ranged from 382.2 to 2993.6 stems ha⁻¹ and basal area spanned 31.8–99.8 m² ha⁻¹; the dominant species, occupying 88% of the basal area of these forests, was *Q. petraea*. Stands were classified into five forest types (Figure 2). Forest types A, B, and D correspond to forests with a high basal area of *Castanea sativa* Mill. However, because of the presence of *Quercus pubescens* Willd., Type D is very different from Types A and B and all other groups. Type A stands have a complex multi-layered structure with high basal areas of *Acer opalus* Mill., *Corylus avellana* L., and *Quercus ilex* L., while in Type B stands the total basal area of companion species is lower and the basal area of *Q. petraea* correspondingly higher. Types C and E had

Table 1. Species composition variables (the basal area) for each forest type obtained with the cluster analysis, and standard error. The number of stands in each type is indicated (n).

Species	Type A		Type B		Type C		Type D		Type E	
	Mean	error	Mean	error	Mean	error	Mean	error	Mean	error
<i>Quercus petraea</i>	22.00	4.19	37.75	8.31	51.54	11.86	40.41	8.19	36.63	8.44
<i>Quercus ilex</i>	1.11	1.87	0.19	0.24	0.36	0.58	2.49	0.46	3.06	2.93
<i>Fagus sylvatica</i>	0.33	0.26	0.04	0.09	0.23	0.52	0.50	0.68	0.63	1.12
<i>Castanea sativa</i>	4.96	5.08	1.37	1.70	0.01	0.03	3.39	2.58	0.08	0.22
<i>Crataegus monogyna</i>	0.00	0.00	0.21	0.67	0.01	0.05	0.04	0.04	0.00	0.00
<i>Acer opalus</i>	1.18	1.71	0.08	0.26	0.46	0.95	3.43	4.84	0.00	0.00
<i>Corylus avellana</i>	0.56	0.87	0.15	0.51	0.11	0.39	0.32	0.42	0.07	0.25
<i>Arbutus unedo</i>	0.00	0.00	0.02	0.08	0.08	0.15	0.00	0.00	0.05	0.18
<i>Ilex aquifolium</i>	0.04	0.10	0.01	0.02	0.11	0.25	0.00	0.00	0.10	0.17
<i>Sorbus aria</i>	0.00	0.00	0.02	0.04	0.03	0.10	0.00	0.00	0.10	0.22
<i>Prunus avium</i>	0.04	0.11	0.00	0.00	0.08	0.29	0.00	0.00	0.30	1.12
<i>Juniperus communis</i>	0.03	0.05	0.03	0.09	0.00	0.00	0.00	0.00	0.10	0.21
<i>Erica arborea</i>	0.00	0.00	0.00	0.00	<0.01	0.02	0.00	0.00	0.36	1.29
<i>Pyrus malus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00
<i>Quercus pubescens</i>	0.00	0.00	0.00	0.00	0.00	0.00	1.24	0.67	0.00	0.00
<i>Abies alba</i>	0.00	0.00	0.00	0.00	<0.01	0.01	0.00	0.00	0.00	0.00
<i>Pseudotsuga menziesii</i>	0.00	0.00	0.00	0.00	<0.01	<0.01	0.00	0.00	0.00	0.00
<i>Fraxinus excelsior</i>	0.00	0.00	0.00	0.00	<0.01	<0.01	0.02	0.04	0.00	0.00
Total	30.21	8.52	39.85	8.76	53.04	12.33	51.87	5.00	41.48	10.09

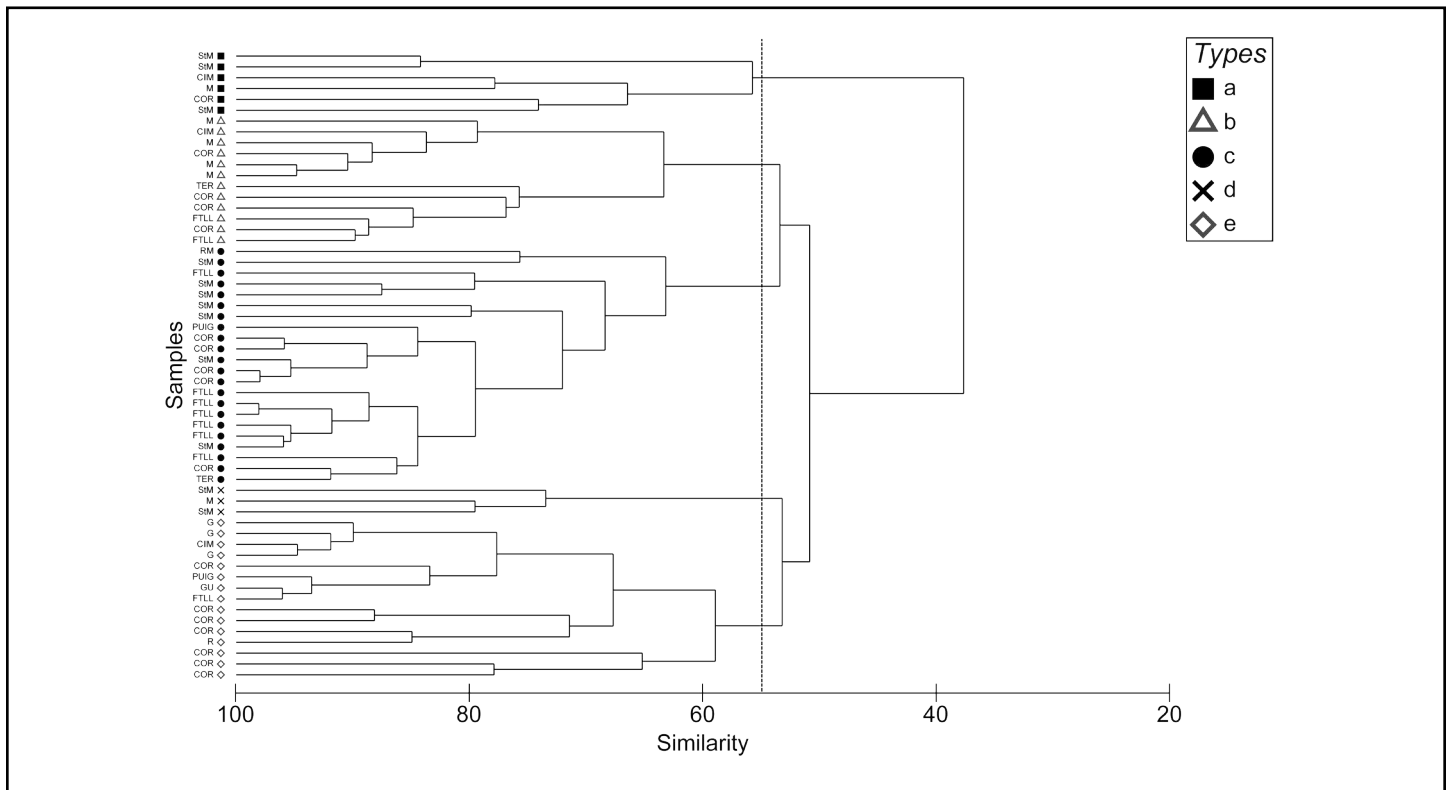


Figure 2. Hierarchical cluster of the species composition (BA) of the sessile oak stands studied. Different forest types are indicated in the key.

much less *C. sativa*. Type E stands had higher basal area of companion species (e.g., *Q. ilex* or *Fagus sylvatica* L.) than Type C stands where *Q. petraea* usually has higher total basal area, but Type C shows a greater richness of companion species. Type C is the largest group, encompassing 40% of the inventoried stands, followed by Types E (26%), B (21%), and A (8%). Type D (5%) occurs on few sites, and most of the stands grow on substrate of phyllite and cornubite.

Forest Parameters

The five forest types exhibit important differences not only in species composition but also in their structure and dynamics (Figure 3). The forest variables are tested with one-way ANOVA (Table 2). The stands of Types C and D have significantly higher total basal area than do the other groups. In Type D this is the result of a high density of stems, but in Type C it is a result of a larger mean dbh of the trees. In addition, Type C, along with Type B, are characterized by a dominance of *Q. petraea* with the companion species not presenting any substantial density or basal area. On the other hand, in Type A and E stands, the density and the basal area of *Q. petraea* are lower and the richness of companion species higher. Type A forests have a significantly lower total density and, as a consequence, the basal area is lower as well. In many of the stands, *Q. ilex* is of minor importance, while in Types D and E the density of the species is significantly higher. As with the basal area, there is a significantly higher density of *C. sativa* in Type A, B, and D stands.

Type D stands (followed by Type B) have the highest mortality values for *Q. petraea* (Table S2), likely because the substrate is less optimal for this species. However, the mortality values among the other groups are similar. There are no significant differences between the groups in terms of height, nor are there any differences in shrub or herbaceous cover (Table S2).

The distribution of the diameter classes (Table 2) in Types A, B, and D indicate young stands. The dominance of small-diameter stems in Types B and D is due to the

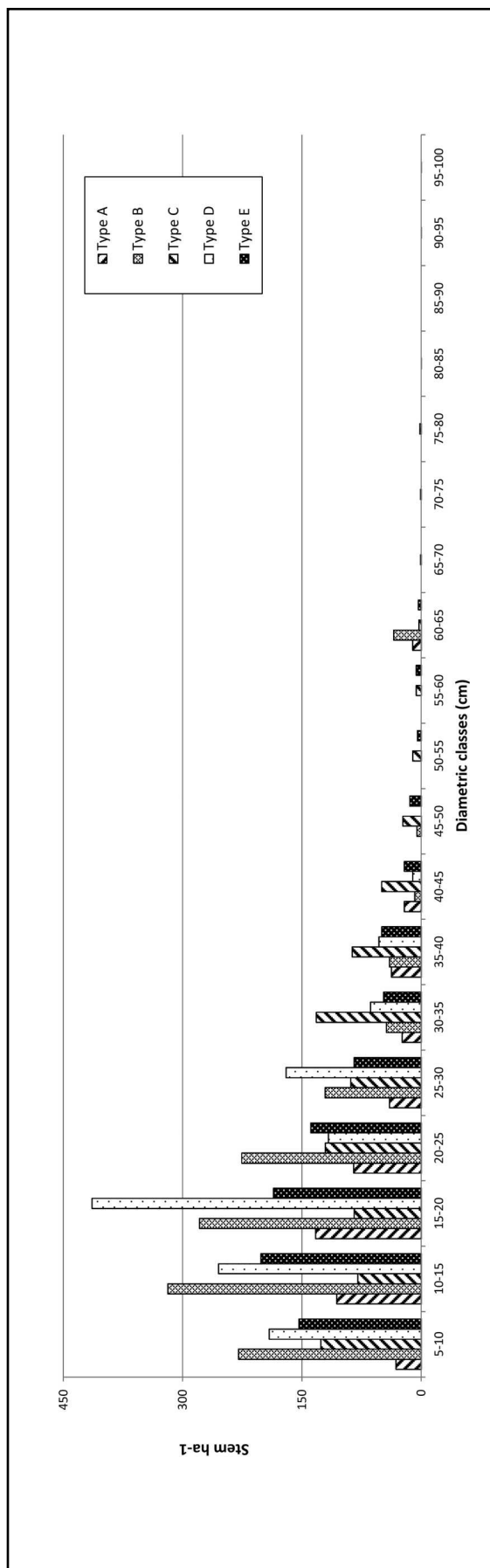


Figure 3. Diametric classes distribution for each forest type, defined by the hierarchical cluster. The y axis shows the tree *Q. petraea* density (stem ha⁻¹) for each diameter class.

Table 2. Forest variables for each forest type obtained with the cluster analysis, and standard deviation. The ANOVA results are shown, and also a Tukey's HSD to show significant differences between forest types.

Forest variables		Type A		Type B		Type C		Type D	
		mean	SD	mean	SD	mean	SD	mean	SD
DBH (cm)	<i>Q. petraea</i> mean	26.65	8.0	20.57	6.1	27.03	6.9	19.12	2.6
	<i>Q. petraea</i> max	45.74	14.9	37.09	7.4	51.31	14.7	38.23	3.2
Density (stem ha ⁻¹)	<i>Q. petraea</i>	488.32	387.3	1263.27	805.1	812.7	264.8	1273.89	589.8
	<i>Q. ilex</i>	63.69	53.3	41.14	52.8	46.32	48.9	424.63	267.1
	<i>C. sativa</i>	130.04	134.5	72.98	81.0	6.04	12.5	116.77	73.5
	<i>C. avellana</i>	148.62	231.1	37.15	128.7	36.19	123.7	74.31	80.1
	Total	942.14	459.8	1491.51	817.5	1034.56	249.9	2186.84	710.2
BA	BA total	30.21	8.5	39.85	8.8	53.04	12.3	51.87	5.0
Diametric classes (stem ha ⁻¹)	<i>Q. petraea</i> 5–25	355.63	439.6	1052.28	893.5	410.38	273.6	976.65	587.5
	<i>Q. petraea</i> 25–45	122.08	81.6	212.31	100.1	357.04	82.1	297.24	66.3
	<i>Q. petraea</i> 45–105	10.62	16.4	39.81	118.5	46.68	67.8	0.00	0.0

significantly lower dbh of *Q. petraea*, but in Type A it results from the high density of *C. avellana*. Types C and E, on the other hand, exhibit a broader range of diameters for *Q. petraea*, with the very large trees being found in Type C.

While there are no large differences in the richness of tree species (Table S2) among the other forest types, Type D stands do possess a considerable wealth of tree species, thanks to the presence of deciduous species. There are no significant differences in shrub richness among the forest types.

Q. petraea regeneration (Table S2) shows a high variability within stands, but there are no significant differences among the types, though regeneration was slightly higher in Type B stands. The regeneration of *Q. petraea* is higher than that of companion species, and there are no significant differences among forest types in the regeneration of companion species. That said, Type E stands do generally exhibit less total regeneration, but this is only marginally significant ($P = 0.05$).

Environmental Factors

The species composition shows an environmental gradient (Figure S1), linked to the hydric stress of the plants, since precipitation ($P = 0.001$), solar radiation ($P = 0.004$), and altitude ($P = 0.001$) have

the opposite effect to maximum ($P = 0.001$), mean ($P = 0.001$), and minimum ($P = 0.001$) temperatures on the similarities of the compositions. There is not a relationship with slope aspect ($P = 0.518$) or slope ($P = 0.443$). Low hydric stress stands encourage Eurosiberian species such as *Sorbus aria* L. Crantz, *Juniperus communis* L., and *C. avellana*, whereas the Mediterranean species like *Arbustus unedo* L. and *Q. ilex* seem to be more commonly found in high hydric stress stands.

Approach to Forest Dynamics

There were clear differences among the forest types in terms of the degree of forestry activity in the first half of the 20th century as mapped by Bou and Vilar (2018; Table 3). The stands can be classified into those that were sparse forest and those that were dense forest in 1956. The forest types can then be ordered according to their inclusion in these two groups (Figure 4). Type A stands were most heavily exploited followed by Type D. Type E has a similar number of exploited and unexploited stands. Finally, Type C and especially Type B showed little evidence of exploitation.

DISCUSSION

Most of the sessile oak forest stands in Montseny show a wide range of diameters for *Q. petraea* (i.e., Types C and E).

Thus, there are very few stands that we can consider as mature forest. This lack of large trees and mature forest in Montseny is a consequence of historical forestry activity (Salvat et al. 2016; Vicens et al. 2016). Type C forests are quite interesting because in Europe stands tend to lose *Q. petraea* dominance when human activity is abandoned (Petritan et al. 2012; Eaton et al. 2016), but *Q. petraea* has remained dominant in Montseny for more than 50 y. Type E stands, however, have less *Q. petraea* and show a tendency toward being mixed forests with *Q. ilex* and *F. sylvatica*.

On the other hand, there are some irregular structures (Types A, B, and D), where diametric classes tend to be small. In Type A stands, companion species have a high density of low-diameter classes, but this is not due to the low density of *Q. petraea*. This forest type had a lot of agro-forestry activity during the first half of the 20th century, and for this reason has a multi-layered structure with a large abundance of *C. avellana*, *A. opalus*, and *Q. ilex*. These stands are usually located on old and abandoned agricultural terraces and have a high density of *C. avellana* in the lower strata and *A. opalus* and *Q. petraea* in the upper strata. Type B stands contain high densities of young trees but in these cases, this is due to the high density of *Q. petraea*. The dense structure leads to high levels of competition, which can increase the mortality rate (Frelich 2002), as hap-

Table 2. (Cont'd)

Type E		ANOVA				TukeyHSD
mean	SD		F	P	Sig	
23.15	8.5	F _{4,53}	26.89	<0.05	*	c-b
44.28	11.7	F _{4,53}	31.87	<0.05	*	c-b
911.18	447.9	F _{4,53}	41.48	<0.01	**	a-b, a-c, a-d, a-e
254.78	200.7	F _{4,53}	74.63	<0.001	***	b-d, b-e, c-d, c-e
7.08	24.6	F _{4,53}	68.16	<0.001	***	c-a, e-a, e-b, d-c, d-e
27.60	90.8	F _{4,53}	1.46	0.23		
1291.22	422.1	F _{4,53}	3.97	<0.01	**	d-a, d-c
41.48	10.1	F _{4,53}	10.49	<0.001	***	c-a, d-a, e-a, c-b, e-c
679.76	526.2	F _{4,53}	21.09	0.09		
202.41	115.2	F _{4,53}	42.96	<0.01	**	c-a, e-c
29.02	33.7	F _{4,53}	14.88	0.22		

pens to *Q. petraea* in some Type B stands.

Understanding forest dynamics is often difficult in places exploited during past eras (Weber et al. 2008)—like the Montseny massif—but our results show that human activity has far-reaching effects on the species composition of several forest groups. Types A and B reveal a great abundance of *C. sativa* because these areas are former chestnut plantations. For many years, forest management extended this type of plantation at the expense of sessile oak (Llobet 1947; Panadera and Nuet 1986). Our results show that the abandoned plantations have been colonized by *Q. petraea* and the sessile oak forest is recovering from this type of human activity.

The density of *Q. petraea* and its companion species in Type A stands has increased over the past 50 y. This process probably began many years ago, when forestry activity in the massif began to be abandoned. Probably abandonment of the forest began earlier in Type B, being dense forests of pioneer species in the 1950s, in that sense similar to current Type A stands. We assume that the pioneer species of Type

A will be replaced by young oaks in the future, converting it to stands similar to Type B today.

Finally, Type D is a prime example of what happens in dry climates like the sub-Mediterranean region. In this case *Q. petraea* tends to mix with *Q. pubescens* and with other drought-tolerant tree species (Eaton et al. 2016). In fact, these two oak species not only compete for water, they sometimes hybridize with each other (Blanco et al. 2005). Most of the stands of Type D were found where the substrate is phyllite and cornubite, being in these cases encountered outside its optimal distribution in Montseny massif (Bou and Vilar 2018).

There are two contradictory studies of what is happening with the sessile oak forest at Montseny. One of them found a decline of *Q. petraea* (Gómez et al. 2008), but this is probably a consequence of the sample because they only studied a small area in a Type E forest. In contrast, a similar-scale study in Type B forest did not show a sessile oak decline (Bou Manobens et al. 2015b). With the current study we analyzed all the sessile oak forest of the Montseny, and we

have to conclude that in this population there is not an oak decline, because the forest shows a recovering dynamic from past impacts.

Generally, the sessile oak forest at Montseny has a similar *Q. petraea* density (921 stems ha⁻¹) to that of the NE Iberian Peninsula (957 stems ha⁻¹), but the basal area is much higher, 41.2 m² ha⁻¹ versus 17.8 m² ha⁻¹, respectively (Terradas et al. 2004), as a result of larger trees in the Montseny forests. Despite a very long history of intensive forestry disturbance, the protection provided by the National Park since 1977 has allowed the forest to recover. It remains important to preserve the park's sessile oak forest as it acts as a reference for the xeric limit populations. Old-growth sessile oak forests are quite rare in Europe (Saniga et al. 2014), and for this reason forest management in Montseny should be focused on conserving mature forests and promoting diameter-class diversity. Furthermore, some of the logging activities observed should be halted. For example, in el Puig, milling was focused only on productivity and not forest sustainability or protection.

Regenerating *Q. petraea* is a problem in some sessile oak forests in Europe (Kotrocó et al. 2012, 2005), so the high abundance of seedlings found in the xeric limit populations of Montseny are evidence that the forest has a promising future in this extreme locality. Other studies concerning the Iberian Peninsula (Vila-Lameiro and Diaz-Maroto 2002) note little regeneration in young stands (Types A and B) and a high level of regeneration in older stands (Types C and E). But in our study, we did not find these dynamics because in Montseny the levels of regeneration do not change as a function of forest age.

Sessile oak forest species composition can change as a function of human activity, but environmental factors also influence

Table 3. Percent occurrence of the stands of each forest type to the vegetation units from 1956 (Bou and Vilar 2018).

Vegetation units in 1956	Type A	Type B	Type C	Type D	Type E
Dense forests	0.00%	83.30%	72.70%	33.30%	46.70%
Sparse forests	100.00%	16.70%	27.30%	66.70%	53.30%

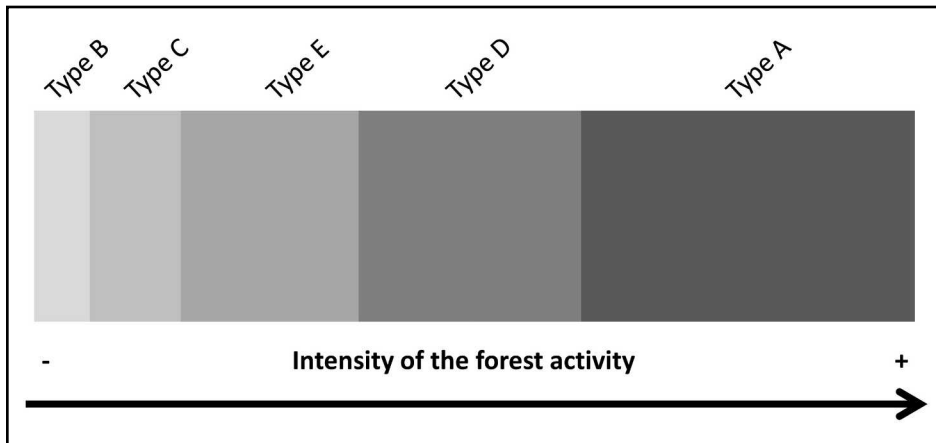


Figure 4. Intensity of the forest exploitation during the first half of the 20th century. To order from least to most intensity, the percent of sparse forest for each forest type has been used.

species abundance. We can separate these factors into climatic and topographic. Of the topographic factors, only altitude affected species composition. It is interesting that while slope aspect does not influence forest composition, it is a limiting factor on the distribution of the sessile oak forest in Montseny massif, which predominantly grows on south-facing slopes (Bou and Vilar 2018). In the wetter regions of the Iberian Peninsula, the distribution of sessile oak forests is not so distinctly limited by slope aspect (Vila-Lameiro and Diaz-Maroto 2002). North-facing slopes in Montseny are occupied by beech forest. Altitude influences many climatic factors and has a direct effect on species composition. Hot, dry stands at low altitude usually include Mediterranean species like *A. unedo* and *Q. ilex*, while cold, wet stands at high altitude have Eurosiberian species such as *S. aria* and *F. sylvatica*, among others. The tolerance of *Q. petraea* for the Mediterranean climate (Blanco et al. 2005) means it is possible to find stands in drier situations in which *Q. ilex* plays an important role in the structure of the forest, and in moister stands where *Q. ilex* is replaced by *F. sylvatica*.

CONCLUSIONS

European countries have reported an extensive decline of their sessile oak forests (Eaton et al. 2016), but the Montseny sessile oak forests depict the opposite dynamic. They are recovering from past

human activity and there is an increase of *Q. petraea* dominance in the forest (e.g., Type B). So, land-use changes have had a significant effect on the current dynamics of the sessile oak forest. Interestingly, Type B has more fully recovered from human impact than Type A. In fact, we believe that in the future, without forest exploitation, the current Type A stands would be similar to the described Type B stands. This is important to bear in mind because, in the context of climate change and with this population being at the xeric limit, we have to suppose that it will be the first to exhibit the impacts of climate change. However, the effect of land-use change may be masking such impacts. So, if we want to understand the future dynamics of the sessile oak forest, we need to incorporate the effects of land-use changes into future studies. We must not underestimate the physiological adaptations of these xeric limit populations to the drought conditions of the Mediterranean region. More studies are needed to understand these xeric limit populations; for example, work on regeneration dynamics to predict the future seedling recruitment or Type E forests to study interspecific competition with *Q. ilex* and *F. sylvatica*.

Forest management will be of vital importance if we want to preserve the sessile oak forest. Xeric limit populations should be conserved, as they are better adapted to water stress and are genetically valuable (Mátyás 2010). We cannot allow the scarce space they currently occupy to be further

reduced because there are only 64 hectares (Bou and Vilar 2018). This is especially the case for Type C forest, where ceasing all logging activities is recommended if we want to preserve and protect these big trees and promote mature forests. Type B forests will probably require adaptive management to combat the effects of climate change, as happens in other forest in Montseny (Sanitjas 2018), because the high density of these stands is an important vulnerability to summer droughts, which involves the increase of hydric stress and probably mortality.

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Table S1. Geographic characteristics of sessile oak forests localities studied in Montseny massif. The number of stands in each locality is indicated "n".

¹Climatic variables were estimated using a georeferenced model (Ninyerola, Pons, and Roure 2000).

²Solar radiation was estimated using a georeferenced model (Pons 1996).

Ref	Locality	UTM 31N	n	Annual rainfall ¹ mm	Mean temp ¹ °C	Min. temp ¹ °C	Max. temp ¹ °C	Solar radiation (m ² *dia* micrometer) ²	Dominant aspect	Mean altitude m a.s.l.	Mean slope
COR	Can Corbera	DG 6723	17	955.3	15.6	5.9	10.7	1536	South	992.7	13.90%
CIIM	Collet de Malcompàs	DG 6827	3	953.3	15.2	6.0	10.5	1357	East	940.5	3.70%
GU	el Guacs	DG 7927	1	913.0	16.4	6.6	11.5	1297	Southeast	785.0	15.00%
PUIG	el Puig	DG 2127	2	979.7	14.0	5.6	9.8	1519	South	1049.5	15.00%
TER	el Terrers	DG 1927	2	950.4	14.4	5.9	10.2	1477	Southeast	992.5	20.20%
FTLL	Fontdellops	DG 9027	10	855.8	17.9	7.3	12.6	1178	Northeast	579.5	6.60%
G	Graners	DG 4828	3	969.7	14.7	5.9	10.3	1251	Northeast	1001.2	2.20%
M	Marmolers	DG 7226	6	934.8	15.6	6.2	10.9	1471	Southwest	898.5	1.70%
R	Ridaura	DG 6322	1	955.9	16.4	6.1	11.2	1490	South	933.3	15.00%
RM	Roureda del Maçaners	DG 5425	1	993.3	13.4	5.3	9.3	1444	South	1178.0	0.50%
StM	Sant Marçal	DG 1727	12	990.8	13.9	5.5	9.7	1469	East	1091.1	10.60%

¹Climatic variables were estimated using a georeferenced model (Ninyerola et al. 2000).

²Solar radiation was estimated using a georeferenced model (Pons 1996).

Table S2. Supplementary forest variables for each forest type obtained with the cluster analysis. Standard deviation (SD) indicated in parentheses. The ANOVA results are shown, and also a Tukey's HSD to show significant differences between forest types.

Forest variables	Type A		Type B		Type C		Type D		mean	SD
	mean	SD	mean	SD	mean	SD	mean	SD		
DBH (cm)	<i>Q. petraea</i> mean	26.65	-8	20.57	-6.1	27.03	-6.9	19.12	-2.6	23.15
	<i>Q. petraea</i> max	45.74	-14.9	37.09	-7.4	51.31	-14.7	38.23	-3.2	44.28
Cover (%)	Shrub cover	27%	-2	30%	-2	32%	-2	26%	-3	35%
	Tree cover	96%	-0.5	94%	-1	96%	-0.4	93%	-0.5	95%
	Herbaceous cover	35%	-3	34%	-3	33%	-2	25%	-3	20%
Regeneration (stem ha⁻¹)	<i>Quercus petraea</i>	118594	-78239.4	269714	-440036	199496	-165674	175208	-211996	71854
	Total	151979	-92365.1	293177	-437995	214606	-167226	229792	-214626	86479
	Companion species	33385.42	-48537.4	23463.54	-23299.2	15110.09	-17880.3	54583.33	-52649.8	
Richness (n° species)	Tree species	4.67	-1	3	-0.7	3.73	-1.9	7.33	-1.5	3.67
	Shrub species	7.67	-2	7.29	-2.5	6	-1.2	7.67	-2.9	6.42
Other	<i>Q. petraea</i> mortality	6%	-1	11%	-1	6%	-1	18%	-1	6%
	<i>Q. petraea</i> height	23.55	-3.6	22.07	-4.3	25.09	-5.3	19.77	-1.1	22.61

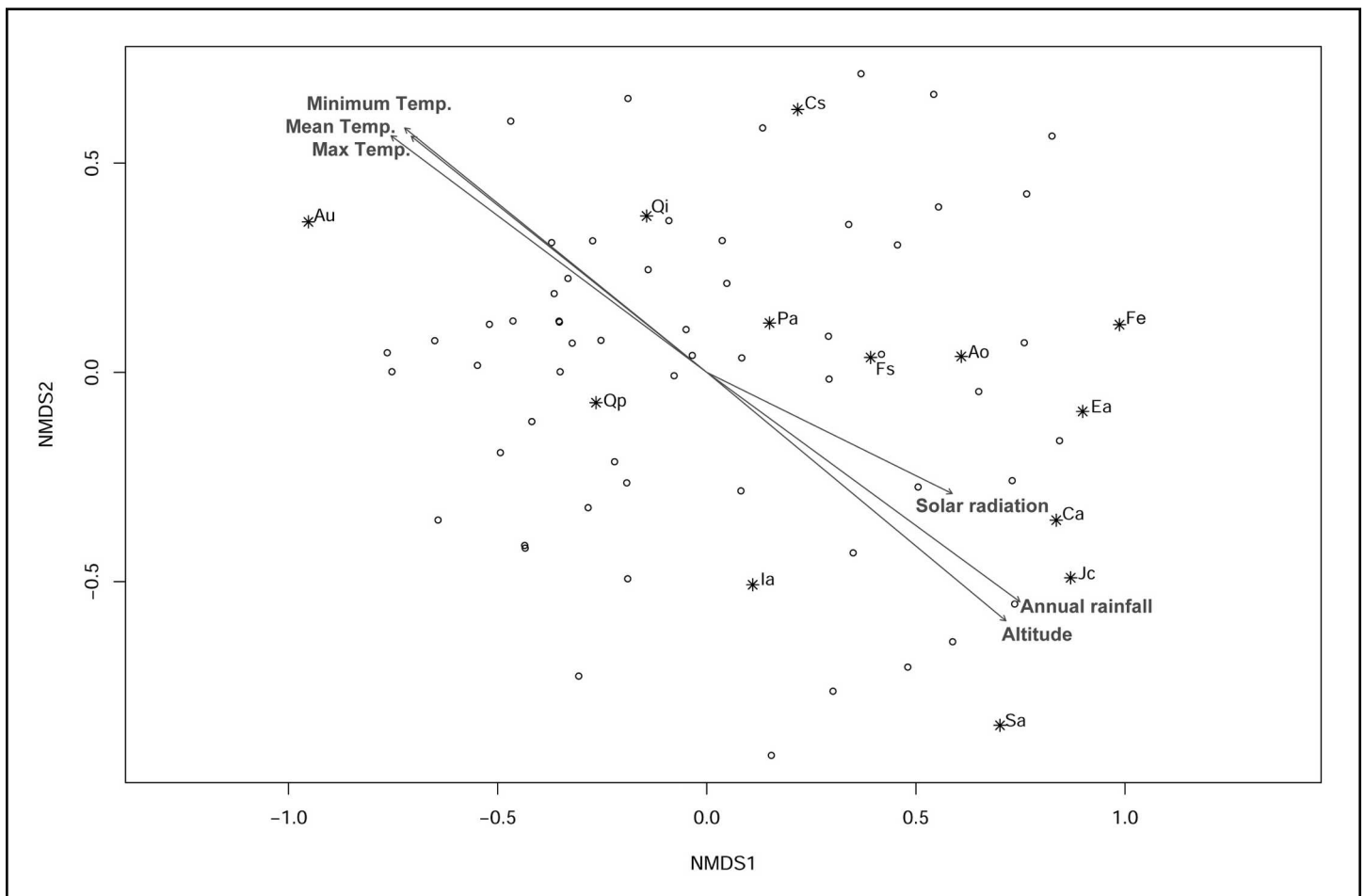


Figure S1. NMDS plot showing stands according to their basal area for each species. The environmental factors with a significant effect ($P \leq 0.05$) are represented by arrows: minimum temperature, mean temperature, max temperature, solar radiation, annual rainfall, and altitude. Acronyms for tree species: Cs (*C. sativa*), Au (*A. unedo*), Qi (*Q. ilex*), Qp (*Q. petraea*), Pa (*P. avium*), Fs (*F. sylvatica*), Ao (*A. opalus*), Fe (*F. excelsior*), Ea (*E. arborea*), Ca (*C. avellana*), Ia (*I. aquifolium*), Jc (*J. communis*) and Sa (*S. aria*).

Table S2. (Cont'd.).

Type E		ANOVA				TukeyHSD
mean	SD		F	P	Sig	
23.15	-8.5	F _{4,53}	26.89	0.04	*	c-b
44.28	-11.7	F _{4,53}	31.87	0.02	*	c-b
35%	-2	F _{4,53}	0.33	0.85		
95%	-0.4	F _{4,53}	12.11	0.32		
20%	-3	F _{4,53}	0.84	0.51		
71854	-58028	F _{4,53}	20.01	0.11		
86479	-67533	F _{4,53}	25.14	0.05		
14625	-17023	F _{4,53}	0.54	0.70		
3.67	-1.9	F _{4,53}	39.53	0.01	**	d-b, d-c, e-d
6.42	-2.2	F _{4,53}	16.20	0.18		
6%	-0.4	F _{4,53}	27.84	0.04	*	d-c
22.61	-7.1	F _{4,53}	0.96	0.44		