

Human impacts drive forest structure and diversity. Insights from Mediterranean mountain forest dominated by *Abies pinsapo* (Boiss.)

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Abstract Environmental factors and land-use are likely interacting to drive forest structure and species diversity, making it difficult to disentangle their separate impacts. Both components influence the resilience and stability of mountain forests in the Mediterranean Basin, since secular land-use has shaped stands structure and forests dynamics are constrained to the environment. Approaches covering environmental factors and contrasting land-uses are still needed to understand their implications on forest dynamics. We investigated patterns of environmental variables, stand structure and biodiversity in forest dominated by *Abies pinsapo* for 61 stands over their whole range. In addition, since land-use by local inhabitant could be a key factor, logging intensity was quantified by stumps basal area and recent land-use history was investigated. Partial redundancy analysis (pRDA) was conducted to assess to which degree the structural attributes are related to environmental characteristics and/or the land-use in the main *A. pinsapo*

forests. Environmental characteristics accounted for 13% of the total variance, while the contrasting land-use (Spain vs. Morocco) and the stumps basal area, as indicator of human logging, accounted for 23% of the total variance. Trees species diversity was near 5 times higher in Moroccan stands than in stands from south Spain. According to recent human logging, Spanish stands have been strictly protected, but Moroccan stands showed widespread axe-logging by local inhabitant over the smaller tree sizes. Our results suggest that the preservation of a minor perturbation regimen by local populations enhance and help to preserve the whole biodiversity of this relict habitat.

Keywords *Abies pinsapo* · Biodiversity · Forest structure · Land-use changes · Mediterranean fir · Partial redundancy analysis · Variance partitioning

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Introduction

Diversity has become an important issue within the discussion of sustainability in the last decade, since the resilience and stability of a forest ecosystem is often linked to the structural and species diversity levels (Lähde et al. 1999; Neumann and Starlinger 2001; Pommerening 2006). A good understanding of the dependencies between biotic, abiotic and human-induced impacts on forest structure and biodiversity is important for the adaptation of forest management activities and conservation measures, especially for endangered tree species (Ruprecht et al. 2009). The Spanish and Moroccan Pinsapo-fir (*Abies pinsapo* Boiss.) forests have been recognized as areas of high biodiversity and endemism (Barbero and Quézel 1975; Medail and Diadema 2009). *Abies pinsapo* is a relict species of the group of the

circum-mediterranean firs. This endemic tree grows in small and isolated populations between 1,000 and 1,800 m a.s.l., in N-facing slopes and ravines of some coastal mountain ranges of southern Spain (West Betic Range) and northern Morocco (Rif Mountains). In south Spain, *A. pinsapo* is currently found in about 3,600 ha, while it accounts for about 3,000 ha in northern Morocco (Linares and Carreira 2009). These forests were intensely damaged over the centuries through a variety of unsustainable practices such as overgrazing, uncontrolled logging and pollarding (Linares et al. 2009). In south Spain, fragmented populations of *A. pinsapo* experienced an expansion and densification from scattered remaining stands following the implementation of conservation measures in the middle of the XX century (Ruiz de la Torre et al. 1994; Linares and Carreira 2009).

The Rif mountains of northern Morocco represent a region of international significance from the standpoint of plant biodiversity with *A. pinsapo* var. *marocana* among the endemic species (Barbero et al. 1990; Médail and Quézel 1999; Médail and Diadema 2009). On this region, the forest clearance, soil erosion, high rural population density and population growth are serious threats. Legal and illegal exploitation of the remaining natural forest and land clearance for the expansion of the cultivated area are nowadays resulting in a loss of natural vegetation cover (Moore et al. 1998).

The need to conserve and restore these relict and endemic fir forests has been increasingly recognized, being, for instance, a priority habitat under the EU Habitat Directive (9,520) and being included in national and regional red lists and protection initiatives. Moreover, since 2006, the Pinsapo-fir forests are included in the Mediterranean Intercontinental Biosphere Reserve of Spain and Morocco, established by the UNESCO's Man and the Biosphere Program. Research studies on endangered tree species usually focus on the environmental conditions of the population, the regeneration status and the causes of declination (García et al. 2000; Zamora et al. 2001). Studies using structural features in order to identify the effects of past human impacts and recent land-use changes on the viability of endangered tree species have not been done so far.

It is widely acknowledged that forest structure is a driving factor behind forests growth processes (Dobbertin 2005; Pommerening 2006; Ruprecht et al. 2009). Moreover, the stand structure and biodiversity of a forest ecosystem can be modified directly by human-use history. Stand structure can range from even-aged, when regeneration occurred as a consequence of a single recruitment event, to all-aged if this was a continuous regeneration pattern (Oliver and Larson 1990). On the other hand, trees biodiversity can range from mono-specific, when a stand is shaped by a single species, to mixed stands, if several trees

species are present (Veblen 1992). In dense temperate forests, regeneration patterns of trees are interpreted to be a consequence of the frequency and magnitude of disturbances that killed one or several dominant canopy trees (Runkle 2000). Land-use history can be also used to assess the long-term effect of anthropogenic activities on disturbance regimes and forest dynamics (Abrams and Orwig 1996). In addition, appropriate application of principles derived from knowledge of stand dynamics might be an important element in successful conservation and restoration of forest ecosystems (Hunter 1990; Ferris-Kaan et al. 1998; Lähde et al. 1999; Edwards and Mason 2006).

The objective of this study was (i) to disentangle the relative contribution of environmental characteristics and the human managing in explaining patterns in the structural attributes of the main *A. pinsapo* forests from south Spain and northern Morocco, and (ii) to discuss the land-use-related processes underlying the stand dynamics. For this purpose, we carried out a structural characterization of several stands, accounting for several sources of variation.

Materials and methods

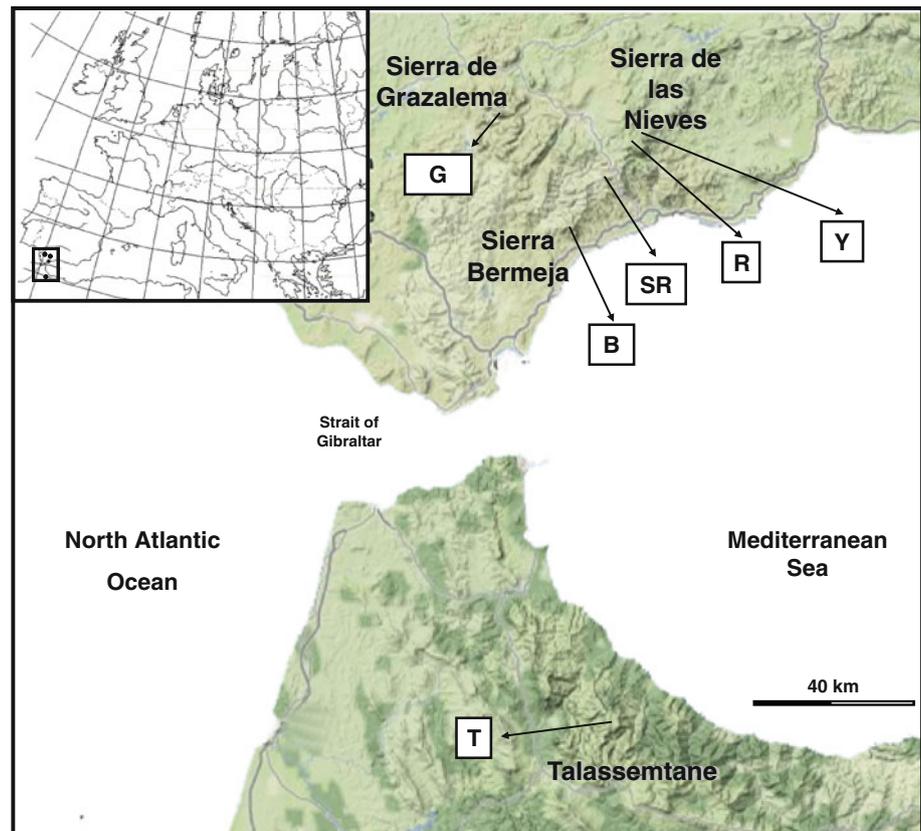
Site description

Our study was conducted at the Mediterranean Intercontinental Biosphere Reserve of Spain and Morocco (Fig. 1). We summarized several field surveys carried out between 2003 and 2007 on five localities of south Spain: Yunquera forests (Y) and Ronda forest (R), both in the Sierra de las Nieves Natural Park; Sierra Real forest (SR); Los Reales de Sierra Bermeja forest (B), in Los Reales de Sierra Bermeja Natural Site; Grazalema forest (G), in the Sierra de Grazalema Natural Park; and one locality in north Morocco: Talassemrane forest (T), in the Talassemrane National Park (Fig. 2). We selected stands not disturbed by intense logging or fires during the last 50 years. Ultrabasic peridotite is the predominant bedrock in Sierra Bermeja and Sierra Real, while calcareous substrates (limestone and dolomite) are the most abundant in Sierra de las Nieves, Sierra de Grazalema and Talassemrane (Figs. 1, 2; Table 1). Serpentine soils at the studied plots on Sierra Real and Sierra Bermeja were mainly mesic Oxiaquic hapludolls, while in the studied plots on Sierra de las Nieves, Sierra de Grazalema and Talassemrane, the soils were mainly mesic Calcic Haploxerepts (Liétor et al. 2003).

Structural analysis

The surveyed area covered more than 95% of the *A. pinsapo* forests. We selected 6 localities and sampled 61 *A. pinsapo* stands in plots of 400–1,000 m² (T, n = 5; G, n = 9; SR,

Fig. 1 Distribution of *A. pinsapo* forests in south Spain and northern Morocco (inset redraw based on Jalas et al. 1999). Study sites locations over calcareous substrates: Talassemrane National Park (T); Sierra de Grazalema (G) and Sierra de las Nieves Natural Park, (Ronda Forest, R, and Yunquera forest, Y). Study sites locations over serpentines substrates: Sierra Bermeja Natural Site (B) and Sierra Real (SR)



$n = 6$; $B = 13$; $R, n = 13$; $Y, n = 15$; see also Table 1) to estimate several environmental (elevation, aspect, soil type, topography), and biotic (canopy structure, overstorey and understorey species composition) variables. We also studied structural variables typically related to the successional stage of the stand (Oliver and Larson 1990). We measured the size of trees (diameter at breast height, dbh) and the density of the stands (basal area and trees per hectare). Shannon's species diversity index was calculated as:

$$H = - \sum_{i=1}^S p_i \ln(p_i),$$

where p_i is the fraction of individuals belonging to the i -th species. For the estimation of structural diversity, the distribution of dbh of each stand was grouped on 10-cm classes, and then H was calculated with p_i as the fraction of individuals belonging to the i -th class of dbh.

Statistical analyses

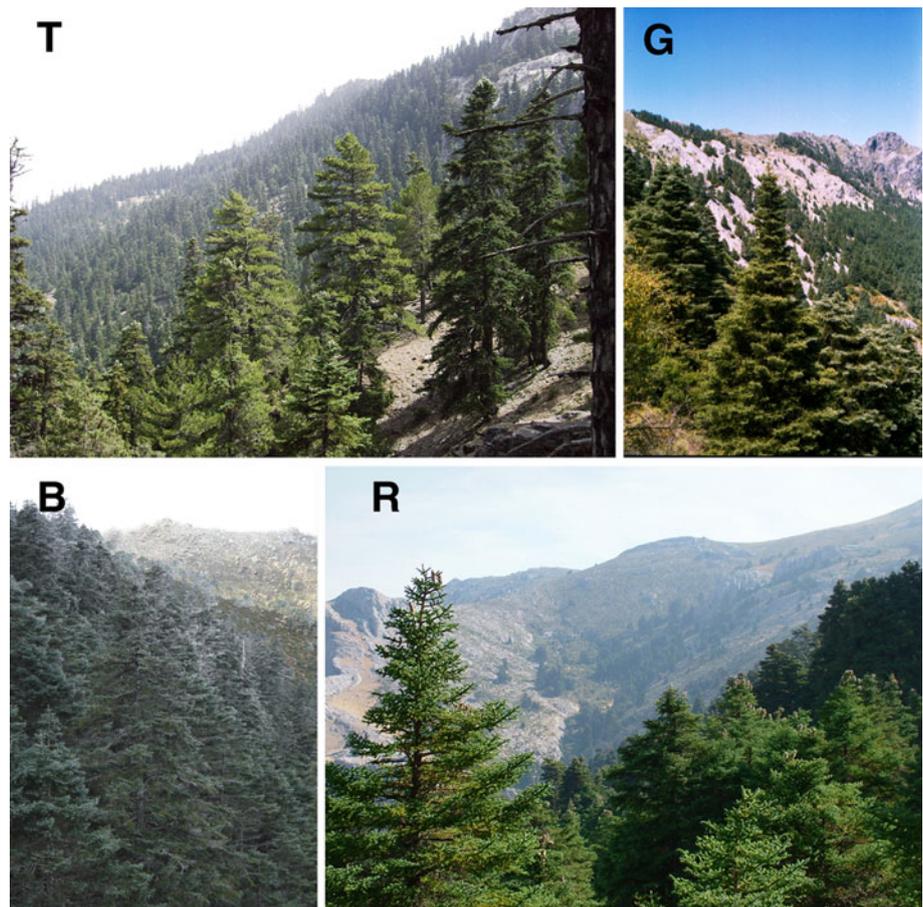
Statistical analyses for mean values of response variables were performed using one-way ANOVA and post hoc Tukey HSD test; the level of significance was fixed as $\alpha = 0.05$. We conducted a partial redundancy analysis (pRDA) to assess to which degree the structural attributes

are related to environmental characteristics and/or the land-use in the main *A. pinsapo* forests (Zuur et al. 2007).

The maximum dbh (Maxdbh), the Shannon diversity index for dbh (H_{dbh}), the stand density (den, expressed as trees per hectare), the mean dbh (mdbh), the variance for dbh (vdbh), the stand alive basal area (livba, expressed as m^2 per hectare), the stand dead basal area (dba, expressed as m^2 per hectare) and the Shannon diversity index for tree species (H_{spp}) were included in the RDA as response variables (thereafter denoted by Y). The explanatory variables were divided into two groups, environmental variables (thereafter denoted by X), which included bedrock (rock, limestone or serpentines), elevation (el), slope (slo) and aspect (asp), and anthropic variables (thereafter denoted by W), which included the contrasting land-use for the two countries (country, Spain or Morocco, as a binary variable) and the stumps basal area as indicator of human logging intensity (stpba, expressed as m^2 per hectare).

Variance partitioning was performed in order to determine the total variance explained, the pure X effect, the pure W effect, the shared effect and the amount of residual variation. For them, the following sequence of steps for variance partitioning in RDA were used: first, we applied a RDA on Y against X and W together; second, we applied a RDA on Y against X; third, we applied a RDA on Y against W; fourth, we applied a partial RDA on Y against X, using

Fig. 2 Landscape pictures of the Mediterranean Intercontinental Biosphere Reserve of Spain and Morocco: Talassemthane forest (T), in north Morocco; Grazalema forest (G), in the Sierra de Grazalema Natural Park; Sierra Bermeja forest (B), in Los Reales de Sierra Bermeja Natural Site; and Ronda forest (R), in the Sierra de las Nieves Natural Park



W as covariates; and fifth, we applied a partial RDA on Y against W, using X as covariates. Using the total sum of canonical eigenvalues of each RDA analysis (which is equivalent to R^2 in regression), the pure X effect, the pure W effect, the shared information and the residual variation can all be explained as a percentage of the total inertia (variation, see Zuur et al. 2007).

Finally, to test which of the single explanatory variables is the most important, we performed a forward selection in the partials RDA. For them, the sum of all canonical eigenvalues was used as a tool to assess the marginal effects, i.e. how well a specific selection of explanatory variables explains the variance for stand structure and biodiversity data.

Land-use history reconstruction

The impact of forest-use changes was deduced by comparing historical records of land-use and canopy disturbance events with the stand structure data. Anthropogenic activities in the forests were compiled from diverse documentary sources. Key events that presumably implied a significant change in the use of the *A. pinsapo* forests were documented from publications dealing with forest

administration and land-use history. Also, a variety of unpublished documents and forest reports were examined. Our bibliographical survey yielded that land-use changed in the study area between the 1950s and the 1970s decades by the adoption of conservation measures. This conservation effort has resulted in an elimination of traditional uses (e.g., logging) with subsequent increases in tree cover within protected areas (Linares et al. 2009). For instance, in the Sierra de las Nieves Natural Park, the fragmented populations of *A. pinsapo* experienced an expansion and densification of the scattered, remaining stands following the implementation of conservation measures in the 1950s, such as the cessation of logging and grazing by domestic animals (Linares and Carreira 2009). In the north of Morocco, the Spanish colonial policy (1912–1956) was characterized by an intense forests management with economic goal, leading to the deterioration of some natural ecosystems. However, the direct impact on Pinsapo-fir forests is not well documented. Although since the 1970s the Moroccan study area was also protected, high rural population density have determined the maintenance of forest clearances, logging, pollarding, grazing and others marginal uses of the remaining natural forest to the present (Taiqui 2005).

Results

The Shannon diversity index estimated for the dbh classes (*H*dbh, Table 1) showed significant differences among the six study areas. Populations from R, G and T showed the wider range of diameters distribution (Fig. 3). In Y stands, about 45% of the trees had a dbh below 15 cm, while in the near R forest the percentage was 4%. T and G stands showed a high percentage of trees in the smaller diameter but wider diameter classes were also present. In contrast, trees wider than 65 cm dbh were absents in SR and trees wider than 40 cm dbh were very rare in Y.

Considering trees species diversity, *T* significantly differed from all the other stands (Table 1). *H* for trees species was near 5 times higher in *T* than in the most biodiverse stands from south Spain (*G* and *BL*). Mortality in the smaller sizes was the highest in G stands, which implies the highest percentage of dead trees (Fig 3) although not a very relevant total dead basal area (table 1).

According to stump basal area, as indicator of recent human logging, *G* stands have been strictly protected, and *SR* and *Y* have received very low human perturbations in the last decades. By opposite, T stands showed widespread axe-logging by local inhabitant in the sizes about 10–15 cm dbh (Fig. 3). In the case of *R* and *B*, the presence of stumps over the whole range of dbh could be due to forest administration clearances after naturally fell of trees, for instance, by storms or snow damages. In any case, the lack of stumps in the smaller diameter classes indicates absence of local inhabitant logging or pollarding. Small-size stumps from *Y* could also be due to past forest administration clearances; higher elevation stands from *Y* (*YH*) showed the lower mean dbh, the higher mean stand density and the lower dead basal area (Table 1 and Fig. 3), which could be related to recent regeneration and absence of human perturbation.

In the T stands, trees diversity was related to the presence of Mediterranean taxa at lower elevation (*Quercus*

Table 1 Characteristics of the studied *A. pinsapo* stands

Country	Morocco	Spain							
	Talassemtane	Grazalema	Sierra Real	Sierra Bermeja		Ronda		Yunquera	
Plots	<i>T</i> (<i>n</i> = 5)	<i>G</i> (<i>n</i> = 9)	<i>SR</i> (<i>n</i> = 6)	<i>BL</i> (<i>n</i> = 5)	<i>BH</i> (<i>n</i> = 8)	<i>RL</i> (<i>n</i> = 4)	<i>RH</i> (<i>n</i> = 9)	<i>YL</i> (<i>n</i> = 8)	<i>YH</i> (<i>n</i> = 7)
Latitude (N)	35.12	36.77	36.62	36.49	36.49	36.72	36.69	36.72	36.73
Longitude (W)	5.42	5.42	4.97	5.20	5.21	5.01	5.03	5.37	4.98
Elevation (m a.s.l.)	1,554	1,138	1,239	1,188	1,431	1,283	1,572	1,195	1,557
Aspect (6: N, 4: NW, 2: NE)	4	4	6	6	6	2	2	6	2
Parent material	Limestone, dolomite	Limestone, dolomite	Peridotite, serpentine	Peridotite, serpentine	Peridotite, serpentine	Limestone, dolomite	Limestone, dolomite	Limestone, dolomite	Limestone, dolomite
Slope (%)	27	31	43	33	45	32	23	25	27
<i>H</i> dbh	2.16	2.24	1.66	1.90	2.20	3.05	2.49	1.74	1.07
<i>H</i> species	1.34	0.29	0.15	0.28	0.00	0.00	0.12	0.11	0.10
Alive basal area (m ² ha ⁻¹)	55.89	46.77	32.12	31.72	18.12	32.18	19.30	34.99	19.15
Dead basal area (m ² ha ⁻¹)	2.61	2.23	3.57	3.50	4.33	7.29	7.55	5.32	0.71
Stump basal area (m ² ha ⁻¹)	9.00	0.00	0.21	3.83	4.26	6.54	3.83	0.38	0.00
Density (trees ha ⁻¹)	807.03	869.02	1,220.67	998.48	300.00	140.00	100.00	1,263.37	1,851.04
Mean dbh (cm)	25.51	20.11	16.69	19.29	28.17	59.26	61.72	17.30	10.10
Median dbh (cm)	22.59	12.91	15.25	16.84	25.09	52.56	61.11	15.57	8.82
Geometric mean dbh (cm)	20.75	14.39	14.89	15.92	24.87	51.52	58.93	15.19	9.31
Variance dbh (cm)	308.71	389.33	75.53	153.64	199.22	874.43	301.45	95.00	22.71
Max dbh (cm)	76.86	95.60	38.46	45.20	64.38	116.25	91.39	62.33	24.30

Number of plots and units are shown between brackets; *L* Lower elevation stands; *H* Higher elevation stands; *H* Shannon index; *dbh*, Diameter at breast height

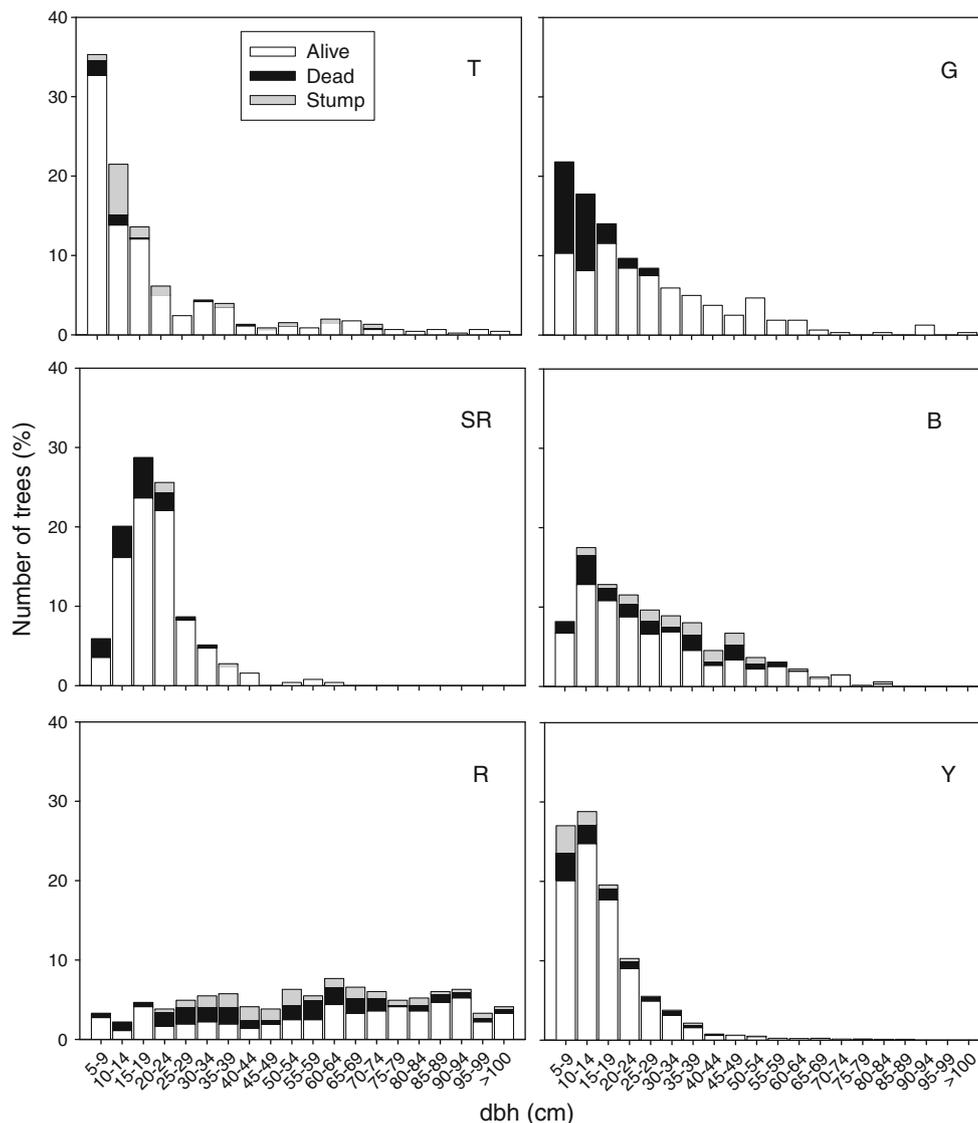


Fig. 3 Diameter class distribution (dbh, cm) for all tree species at Talasemtane (T), Sierra de Grazalema (G), Sierra Real (SR), Sierra Bermeja (B), Ronda (R) and Yunquera (Y) forests

ilex, *Q. faginea*) and to Mediterranean mountain conifers at higher elevation (*Cedrus atlantica*, *Pinus nigra* subsp. *mauretanica*, *Taxus baccata*, etc.). G stands also showed mixed stands with *Quercus ilex* and *Q. faginea*. Serpentine stands (SR and B) also showed at lower elevation mixed stands, in this case with *Pinus pinaster* var. *acutisquama*.

Results of various RDA and partial RDA analysis for environmental and anthropic explanatory variables appear in Table 2. The pure environmental effect is equal to 13% of the variation, while the variance accounted for land-use variables was 22.8% (Table 2). The variance partitioning is presented in Table 3. The shared amount of variation was 0.5%, which indicates that environmental variables are not collinear with anthropic variables. Variance decomposition

yielded the effect of anthropic variables is more important than that environmental ones.

Figure 4a shows the relationships between environmental variables as explanatory ones and structure and diversity as response variables after filtering out the effects of contrasting land-use as covariable. The same analysis is shown in Fig. 4b for the anthropic variables after filtering out the effects of environmental ones. This was done by regressing the covariables and continuing with the residuals as new explanatory variables. Additionally, the covariables are regressed on the canonical axes and the algorithm continues with the residuals as new scores.

After filtering out the effects of land-use, elevation is positively related to tree species diversity, stand density

Table 2 Results of various RDA and partial RDA analysis for environmental and anthropic explanatory variables

Step	Explanatory variables	Explained variance (%)
1	Environmental and anthropic variables	36.3
2	Environmental variables	13.4
3	Anthropic variables	23.3
4	Environmental variables with anthropic variables as covariable	13.0
5	Anthropic variables with Environmental variables as covariable	22.8

Total variation (named inertia) is 1. Percentages are obtained by dividing the explained variance by total variance

Table 3 Variance decomposition showing the effects of environmental and anthropic variables

Component	Explanatory variables	Explained variance (%)
A	Anthropic variables	22.80
B	Environmental variables	13.00
C	Shared (3–5)	0.50
D	Residual	63.70
Total		100

Components A and B are equal to the explained variances in steps 5 and 4, respectively, of Table 2. C is equal to variance in step 3 minus variance in step 5 of Table 2, and D is calculated as total variance (which is equal to 1) minus the explained variance in step 1 of Table 2

and basal area of alive trees (Fig. 4a). Diversity for dbh classes was related to variance in dbh, maximum dbh and dead basal area. Slope and parent material were not very related to any of the remaining variables. The marginal effects of the environmental variables yielded that only elevation and aspect provide a significant increase in the total sum of eigenvalues when they are included as new variable (Table 4).

Removing the effects of measured environmental variables, stumps basal area was positively related to maximum, variance and diversity for dbh, and to basal area for alive trees (Fig. 4b). Based on marginal effects, both land-use-related variables showed a significant increase in the total sum of eigenvalues when they are included in the model (Table 5).

Discussion

Due to intense historical and contemporary land-use, many of the forested areas in the Mediterranean basin are concentrated in mountainous areas. Top-mountain areas around the Mediterranean basin are refuges for relict conifer tree species (e.g., circum-mediterranean fir species) as well as for genetically valuable, isolated populations of tree species whose core-distribution range is located at higher latitude, in temperate regions (e.g., *Pinus sylvestris*, *T. baccata*). Thus, to some extent, these areas represent

temperate-like biome “islands” within the Mediterranean-type climate region (Arista 1995; Linares and Carreira 2009). On the other hand, the areas supporting endemic mountain conifer forests have experienced strong land-use changes during the last decades: abandonment of traditional uses along with the adoption of protection measures (Linares and Carreira 2009; Linares et al. 2009). These have often been rather intensive, because of the high conservation value of these forests, their limited area of distribution and the low overall economic impact of their traditional uses (Carreira et al. 2009).

Since the onset of the 1950 decade, the traditional use of *A. pinsapo* forests by local inhabitants (tree pollarding, charcoal production and uncontrolled grazing) was severely restricted in Spain, following the carrying out of state protection measures (Alvarez Calvente 1994). In a first phase, protection measures were frequently addressed to foster natural regeneration and/or to reforestation tasks focused on the reconstruction of spatial patterns derived from potential vegetation models. Thereafter, no-management or minimum-management options have been commonly applied in the Spanish territories occupied by these forests (IPCC 2007; Linares and Carreira 2009) as showed by the low presence of stumps and the high stand densities. However, over the Moroccan populations remains nowadays a minor-perturbation regimen exerted by rural inhabitants (Taïqui 2005), which could be related to the lesser densification of these forests during the last decades, their higher canopy structural diversity at the stand level and their higher biodiversity (Table 1, Fig. 4). In addition, the Moroccan fir forests not only harbor a higher number of woody species, as we have quantified here, but most of them are endangered, relicts and endemic species (for instance *C. atlantica*), or are at their southernmost distribution range (for instance *Ilex aquifolium*, *T. baccata*, and *Pinus nigra*).

A quantitative description of forest structures could be useful for a wide range of applications in modern forest management and biodiversity research (Ruprecht et al. 2009). Structural diversity is an important indicator for understanding the tree species distribution, individual growing conditions and relations in competition within a

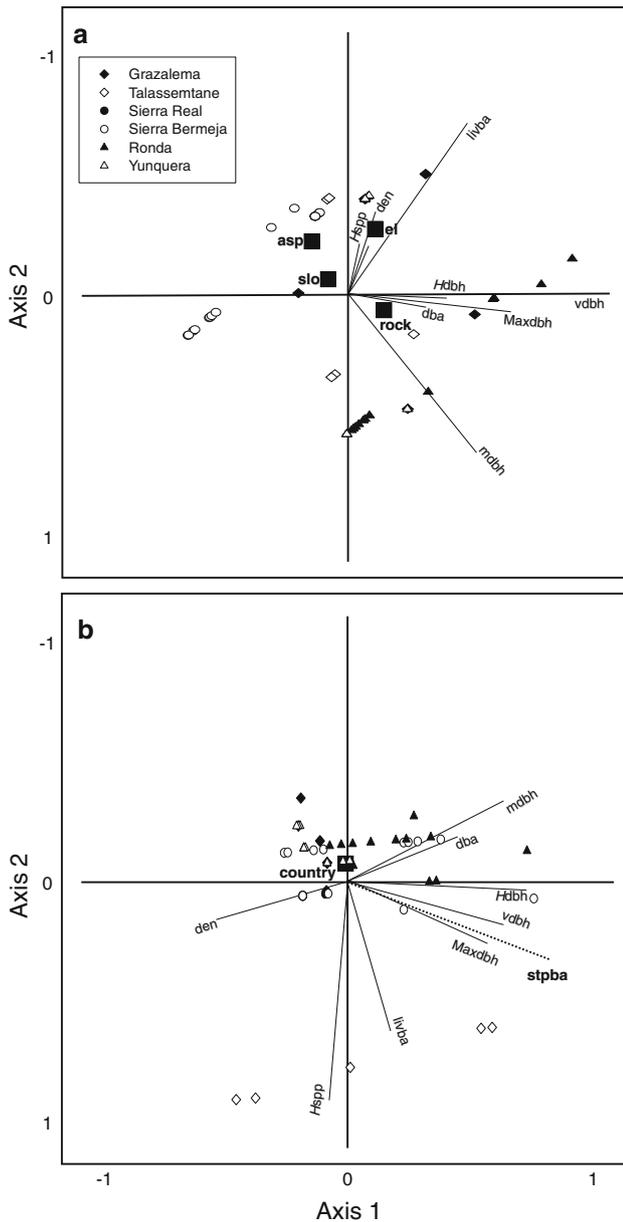


Fig. 4 Effect of environmental variables when the effects of anthropic ones are removed from the response variables (a). In the Fig. 4b, the effect of environmental variables is removed from the response variables and the effects of anthropic variables are shown. The response variables (structural- and diversity-related stand features) are represented by lines and the following labels: Maxdbh (maximum dbh), Hdbh (Shannon diversity index for dbh), den (stand density, trees per hectare), mdbh (mean for dbh), vdbh (variance for dbh), livba (stand alive basal area, m² per hectare), dba (stand dead basal area, m² per hectare) and Hspp (Shannon diversity index for tree species). The quantitative explanatory variable (stumps basal area, stpba) is represented by dotted line and the qualitative (nominal) explanatory variables by squares and the following labels: rock (bedrock), el (elevation), slo (slope), asp (aspect) and country (Spain or Morocco). The samples are represented by dots following the legend inset

forest stand (Pommerening 2002). However, the accuracy achieved for small sample sizes does not allow interpreting biodiversity pattern as an estimate for the whole management unit. Previous studies are mostly focusing on one single population (see Arista 1995) missing the opportunity to compare the similarities and differences among contrasting land-use history and environmental conditions and their effect on the viability of Pinsapo-fir populations (Linares and Carreira 2009). Although the study area showed quite different environmental conditions, it was found that stand structure and biodiversity are not strongly related to variables as parent material or slope (see Table 4), which allowed us to draw some general conclusions on the long-term effect of anthropogenic activities, as traditional logging intensity, on disturbance regimes and forest dynamics (Abrams and Orwig 1996). This study's findings support the ongoing discussion that conventional conservation strategies may not be sufficient in order to maintain a population of slow growing, long living tree species predicted to be in long-term decline (Ruprecht et al. 2009). In this context, the analysis of the relationship between the structural diversity of Pinsapo-fir forests and environmental and land-use features allows one to adapt conservation management strategies (Montes et al. 2005). The structural attributes of forest stands are increasingly recognized as being of theoretical and practical importance in the understanding and management of forest ecosystems. This is because structure is the attribute most often manipulated to achieve management objectives following the establishment of a forest stand (Franklin et al. 2002).

The pRDA method allowed us to disentangle the relative contribution of measured environmental and land-use-related variables. Our findings support land-use has the potential to profoundly change the structure and dynamics of tree populations. Both environmental and land-use-related variables are certainly interacting, but the obtained disentangle of their separate impacts shows a higher relative contribution of human managing, compared to environmental features (see Table 3). Secular land-use has shaped forest structure in Mediterranean mountains, which would have substantial implications for the restoration and management of *A. pinsapo* forests. Restoration of native forests and management of forest dynamics in nature areas are increasingly considered as priorities in forestry and environmental policies. However, land abandonment has also played a major role in promoting large continuous areas of dense and uniform early-successional vegetation (Ferris-Kaan et al. 1998), which could lead to low growth rates and some decay symptoms by stand stagnation (Linares and Carreira 2009). By opposite, successful natural regeneration could be promote by low intensity

Table 4 Marginal effects for the environmental variables after the effects of anthropic ones were removed (see Fig 4a)

Variable	Eigen value using only one explanatory variable	Eigen value as % of sum all eigenvalues using only one explanatory variable	Conditional effects: Increase total sum of eigenvalues after including new variable	<i>F</i>	Statistic <i>P</i> -value
Bedrock	0.045	35.89	0.01	1.15	0.314
Elevation	0.036	32.65	0.05	4.52	0.008
Slope	0.006	8.18	0.01	1.09	0.309
Aspect	0.047	40.42	0.05	4.31	0.007

The total sum of all eigenvalues is 0.134, and the total variance is 1. *F*-test and *P*-value were also shown

Table 5 Marginal effects for the anthropic variables after the effects of environmental ones were removed (see Fig 4b)

Variable	Eigen value using only one explanatory variable	Eigen value as % of sum all eigenvalues using only one explanatory variable	Conditional effects: Increase total sum of eigenvalues after including new variable	<i>F</i>	Statistic <i>P</i> -value
Country	0.10	41.09	0.10	8.54	0.002
Stumps basal area	0.13	56.67	0.13	9.82	0.001

The total sum of all eigenvalues is 0.233, and the total variance is 1. *F*-test and *P*-value were also shown

logging by local inhabitant and low browsing intensity, as we have assessed on Moroccan stands. These minor perturbation regime could generate small gaps and areas with a not very dense overstorey cover and promote stand biodiversity (Fig. 4). Meanwhile, the strictly protected *A. pinsapo* stands are the ones showing poor structure-diversification and low biodiversity. On summary, our results suggest that the preservation of minor perturbation regimes by local human populations would also help to preserve the whole biodiversity of this relict habitat.

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References

- Abrams MD, Orwig DA (1996) A 300 year history of disturbance and canopy recruitment for co-occurring white pine and hemlock on the Allegheny Plateau, USA. *J Ecol* 84:353–363
- Alvarez Calvente M (1994) Los pinsapares malagueños en el recuerdo. In: Gestión y conservación de los pinsapares andaluces pp 77–90. Asociación forestal andaluza
- Arista M (1995) The structure and dynamics of an *Abies pinsapo* forest in Southern Spain. *For Ecol Manage* 74:81–89
- Barbero M, Quézel P (1975) Les forets de Sapin sur le pourtour méditerranéen. *Anal Inst Bot Cabanilles* 32:1245–1289
- Barbero M, Bonin G, Loisel R, Quézel P (1990) Changes and disturbances of forest ecosystems caused by human activities in the western part of the mediterranean basin. *Vegetation* 87: 151–173
- Carreira JA, Quintanilla J, Linares JC (2009) Conservation and management adaptation options for the in situ preservation of endemic mountain conifer forests: the *Abies pinsapo* case in Andalusia (Spain). In: Mediterranean mountains in a changing world. Guidelines for developing action plans pp 57–61. IUCN, Gland, Switzerland and Málaga, Spain
- Dobbertin M (2005) Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur J Forest Res* 124:319–333
- Edwards C, Mason WL (2006) Stand structure and dynamics of four native Scots pine (*Pinus sylvestris* L.) woodlands in northern Scotland. *Forestry* 79:261–277
- Ferris-Kaan R, Peace AJ, Humphrey JW (1998) Assessing structural diversity in managed forests. In: Bachmann P, Kohl M, Paivinen R (eds) Assessment of biodiversity for improved forest planning. Kluwer Academic Publishers, Dordrecht, pp 331–342
- Franklin JF, Spies TA, Van Pelt R (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using douglas-fir forests as an example. *For Ecol Manage* 155:399–423
- García D, Zamora R, Hódar JA, Gómez JM, Castro J (2000) Yew (*Taxus baccata* L.) regeneration is facilitated by fleshy-fruited shrubs in Mediterranean environments. *Biol Conserv* 95:31–38
- Hunter ML (1990) Wildlife, Forests, and Forestry: Principles of Managing Forests for Biological Diversity. Prentice-Hall, NJ
- IPCC (2007) Afforestation, reforestation, and deforestation (ARD) Activities. In: IPCC special report on land use, land-use change and forestry
- Jalas J, Suominen J, Lampinen R (1999) Atlas florae europaeae. Cambridge University Press, Cambridge
- Lähde E, Laiho O, Norokorpi Y, Saksa T (1999) Stand structure as the basis of diversity index. *For Ecol Manage* 115:213–220
- Liétor J, Linares JC, Martín-García JM, García-Ruiz R, Carreira JA (2003) Relaciones suelo-planta en bosques de *Abies pinsapo* Boiss. Disponibilidad de nutrientes y estatus nutricional. *Acta Botánica Malacitana* 28:89–104
- Linares JC, Camarero JJ, Carreira JA (2009) Interacting effects of climate and forest-cover changes on mortality and growth of the

- southernmost European fir forests. *Glob Ecol Biogeogr* 18: 485–497
- Linares JC, Carreira JA (2009) Temperate-like stand dynamics in relict Mediterranean-fir (*Abies pinsapo*, Boiss.) forests from Southern Spain. *Ann For Sci* 66:610
- Medail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *J Biogeogr* 36:1333–1345
- Médail F, Quézel P (1999) Biodiversity hotspots in the Mediterranean basin: setting global conservation priorities. *Conserv Biol* 13: 1510–1513
- Montes F, Sánchez M, del Río M, Cañellas I (2005) Using historic management records to characterize the effects of management on the structural diversity of forests. *For Ecol Manage* 207:279–293
- Moore HM, Fox HR, Harrouni MC, El Alami A (1998) Environmental challenges in the Rif mountains, Northern Morocco. *Environ Conserv* 25:354–365
- Neumann M, Starlinger F (2001) The significance of different indices for stand structure and diversity in forests. *For Ecol Manage* 145:91–106
- Oliver CD, Larson BC (1990) *Forest stand dynamics*. McGraw-Hill, New York, p 467
- Pommerening A (2002) Approaches to quantifying forest structures. *Forestry* 75:305–324
- Pommerening A (2006) Evaluating structural indices by reversing forest structural analysis. *For Ecol Manage* 224:266–277
- Ruiz de la Torre J, García JJ, Oria de Rueda JA (1994) Gestión y conservación de los pinsapares andaluces. Asociación forestal andaluza
- Runkle JR (2000) Canopy tree turnover in old-growth mesic forests of Eastern North America—statistical data included. *Ecology* 79:1768–1780
- Ruprecht H, Dhar A, Aigner B, Oitzinger G, Klumpp R, Vacik H (2009) Structural diversity of English yew (*Taxus baccata* L.) populations. *Eur J For Res* 129:189–198
- Taïqui L (2005) Evolution récente de la structure du paysage du bassin de Chefchaouen (1958–1986). In: *Mutations des milieux ruraux dans les montagnes rifaines (Maroc)*. G.R.G.Rif Ed., Tétouan
- Veblen TT (1992) Regeneration dynamics. In: Glenn-Lewin DC, Peet RK, Veblen TT (eds) *Plant succession: theory and prediction*. Chapman and Hall, London, pp 152–187
- Zamora R, Gómez JM, Hódar JA, Castro J, García D (2001) Effect of browsing by ungulates on sapling growth of scots pine in a Mediterranean environment: consequences for forest regeneration. *For Ecol Manage* 144:33–42
- Zuur AF, Ieno EN, Smith GM (2007) *Analysing ecological data*. Springer, New York, p 672