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Changes in the structure and composition of two *Pinus nigra* subsp. *salzmannii* forests over a century of different silvicultural treatments

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Abstract

Silvicultural treatments imply the felling of trees, which can modify species composition and structural diversity. Consequently, it is important to assess the influence of silvicultural treatments on forest composition and structure. The principal objective of this study was to analyze changes in the composition and structural diversity of two forests: Los Palancares y Agregados (Cuenca Mountain Range, Central-east of Spain) and Navahondona (Cazorla Mountain Range, Southeast of Spain), managed under two different silvicultural methods, i.e. shelterwood and selection. Forest inventory data, covering nearly a century of forest management, were used to follow changes in the number of trees and standing volume. Shannon's index was computed for tree species composition and diameter classes, considering forest comparments as sampling units. Diversity profiles were constructed to follow changes in horizontal diameter class diversity. A partial redundancy analysis (pRDA) was conducted to asses the relative contribution of silvicultural treatments in explaining differences in the current structure of the two study forests. Results showed that silvicultural treatments favoured Spanish black pine and did not benefit other tree species. The number of large trees and the values of Shannon's index decreased in both forests over the study period, but the forest under the uneven-aged silvicultural method showed higher values for both variables. Implications for sustainable forestry are discussed.

Key words: Shannon's index; veteran trees; diversity profiles; biodiversity; adaptive management; shelterwood method; selection method.

Resumen

Cambios en la estructura y composición de dos bosques ordenados de *Pinus nigra* subsp. *salzmannii* durante un siglo de tratamientos selvícolas diferentes

Los tratamientos selvícolas implican la corta de árboles y esto puede modificar la composición y diversidad estructural del bosque. En consecuencia, es importante evaluar la influencia de los tratamientos selvícolas en la composición y estructura de los bosques aprovechados. El objetivo principal de este estudio fue analizar los cambios en la composición y diversidad estructural de dos montes: Los Palancares y Agregados (Serranía de Cuenca, España central) y Navahondona (Sierra de Cazorla, sureste de España), gestionados mediante aclareos sucesivos y entresaca, respectivamente. Se utilizaron datos procedentes de inventarios forestales, que cubrían casi un siglo de gestión forestal, para seguir cambios en el número de árboles y el volumen en pie. El índice de Shannon se calculó para la composición de especies arbóreas y para clases de diámetros, considerando los cantones forestales como unidades de muestreo. Se construyeron perfiles de diversidad para seguir cambios en la distribución de clases de diámetro. La contribución relativa de los tratamientos selvícolas para explicar las diferencias actuales en la estructura de los dos bosques estudiados se evaluó mediante un análisis de redundancia (RDA). Los resultados mostraron que los tratamientos selvícolas favorecieron a *Pinus nigra* y no beneficiaron a otras especies. La cantidad de árboles de grandes dimensiones y los valores del índice de Shannon decrecieron en ambos montes a lo largo del periodo estudiado, pero el bosque gestionado por entresaca presentó valores más altos para las dos variables. Se discuten las implicaciones para la gestión forestal sostenible.

Palabras clave: índice de Shannon; árboles extramaduros; perfiles de diversidad; biodiversidad; gestión adaptativa, entresaca; aclareo sucesivo.

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Introduction

Since forestry science originated in Central Europe towards the end of the eighteenth century, there has been an evolution from an almost exclusive interest in the yield of timber to a major concern in the preparation of management plans which aim to produce timber whilst maintaining forest biodiversity (Hunter, 1999). Under this new paradigm of forestry science, knowledge about both biodiversity atributes [composition, structure and funtion (Noss, 1990)] and the way long-term forest mangement modifies them is essential. In comparison, the ecology of Spanish Mediterranean forests has been widely studied so far (Zamora and Pugnaire, 2001; Valladares, 2004), while it is now that the impacts of forest management on biodiversity atributes are being investigated (Montes *et al.*, 2005; Bravo *et al.*, 2010; Urbieta *et al.*, 2008).

Whatever the aim, forest management normally implies the felling of trees in order to control the establishment, growth and structure of forest stands. By cutting trees down, foresters influence some ecosystem processes at various spatio-temporal scales (*e.g.* mortality rates of tree species or the frecuency of disturbances in given sites) and modify the composition and structure of forest stands (*e.g.* favouring some tree species or grouping harvesting operations in some stands). Then, the monitoring of temporal changes occuring in the composition and structure of exploited forests seems a proper method for analysing the long-term influence of forestry practices on forest biodiversity. Indeed, structural diversity can indicate overall species diversity, as shown in studies about plant, avian and insect diversity (Jonsson and Jonsell, 1999; DeGraff *et al.*, 1998; Kirby, 1992). For instance, Tellería *et al.* (1992) found a positive correlation between trunk density and passerine richness in Spanish forests.

Stand structure includes trees of different species, sizes and conditions, and their spatial arrangement (Franklin *et al.*, 2002). This makes a complex concept of stand structure, so that quantitative comparisons between forest stands can require multivariate analysis or, alternatively, the use of indices devised to express structural complexity as a single number (for a review see McElhinny *et al.*, 2005). Among the variety of indices available for this purpose, species diversity indices have gained wide acceptance in forestry and, perhaps, Shannon's index is the most commonly used one (Staudhammer and LeMay, 2001). It is defined as follows:

$$H' = -\sum_{i=1}^{S} pi \ln pi \qquad [1]$$

where pi is the proportion of individuals in the i^{th} species, and S is the number of species (Magurran, 1988). Here, «species» is a convenient term for the categories into which we place individuals, *i.e.* either tree species or diameter classes can be thought of as «species».

Despite on its popularity, Shannon's index has got some problems in describing forest structure. In first place, equation [1] does not consider size variability and condition of trees within each species, but abundance of tree species and variation in tree size, age and genetic composition are the most relevant components of diversity in a forest stand (Lähde *et al.*, 1999). To overcome this inconvinient, Staudhammer and LeMay (2001) proposed an extension of the Shannon index of diversity by averaging the values of Shannon's indices calculated separately for species and diameter and height classes.

On the other hand, the maximum value of Shannon's index occurs when the proportions are equal over all species. Working with diameter classes, it means that the most diverse stand would be one with an equal number of trees in each diameter class. However, this is not a natural or desirable forest structure, because a bigger number of thin (young) trees is expected in forests with continuous regeneration and healthy stand replacement. This inconvinient can be overcome expresing proportion of a species on metrics of basal area instead of number of individuals. Moreover, calculations should be carried out with the most important control variable used to make management decisions, *i.e.* basal area (Solomon and Gove, 1999).

Finally, all the species weigh equally in equation [1]. This can advoid direct comparisons between diameter distributions. For example, a stand with a 70% of large trees and a 30% of thin trees will come out with the same value of the Shannon's index that another stand with a 70% of thin trees and a 30% of large ones. Yet the biological significance of each stand would be different and so would its meaning for a forester. The number of trees exceeding a threshold diameter, *i.e.* the number of large trees, has been used to characterize the structure of a broad variety of forest types, and can complement the information provided by the Shannon's index (McElhinny *et al.*, 2005). Ideally, the threshold used to distinguish between large and non-large trees should be established on some sort of ecological basis.

Together with the temporal evolution of structural indices, the occurrence of change in the composition and structure of forest stands can be monitored by diversity profiles. Thus, diversity profiles have been used to compare the diversity of species and horizontal structure in remeasured plots in silviculturally treated even-aged and uneven-aged forest stands (Solomon and Gove, 1999).

In this study, we focus on two *Pinus nigra* subsp. *salzmannii* forests, one managed under the shelterwood silvicultural method and the other managed under the selection method. The two studied forest have been felled following prescriptions from management plans since 1890s and a number of consecutive forest inventories have been carried out to present. Despite continuous harvesting over the 20th century, both forests have maintained or increased their growing stock, but little is known about the impact of management on their forest structure (Appendix 1). We used data from the forest inventories to adress the following questions: (1) have management left an imprint on current forest composition? (2) how has stand structure varied over the time forest management is being applied? (3) what is the relative contribution of silvicultural treatments in explaining differences in the current structure of the two study forests?

Material and methods

Species and study sites

Spanish black pine (*Pinus nigra* Arn. subsp. *salzmannii* Dunal (Franco), *Pinus nigra* hereafter) is a Mediterranean pine species. It mainly thrives along the eastern calcareous mountains of Spain, where covers 405983 hectares of pure stands. This study focused on two black pine forests: 'Navahondona forest' (Navahondona hereafter) located at Cazorla Mountain Range (Southeast Spain), and 'Los Palancares y Agregados forest' (Palancares hereafter) located at Cuenca Mountain Ranges (Central Spain, Fig. 1). *Pinus nigra* is the most abundant species in both forests. *Juniperus thurifera* at Palancares, *Pinus pinaster* and *P. halepensis* at Navahondona, and *Quercus ilex* and *Q. faginea* at both Navahondona and Palancares are the most frequent companions of Spanish black pine in those localities where it mixes with other tree species in the study areas.

Rock parent material is Cretaceous limestone at both sites, and soils are calcium rich and mainly shallow.

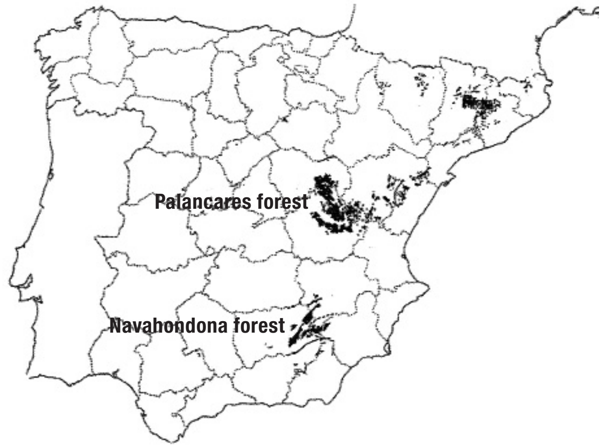

Figure 1. Natural distribution area of *Pinus nigra* subsp. *salzmannii* in the Iberian Peninsula and situation of the two study forests.

According to climatic data for the period 1951-1999 obtained from the «Digital Climatic Atlas of the Iberian Peninsula» (Ninyerola *et al.*, 2005), the two study locations have a Mediterranean type climate. The average annual rainfall in Navahondona is 1271 mm, of which 86 mm occur during the summer. Mean monthly temperature ranges from 2.7°C in January to 20.6°C in August. Intensity of aridity (K) is 0.078 and duration of aridity (A) 2.5 months. In Palancares, the average rainfall is 796 mm, of which 94 mm occur during the summer. Mean monthly temperature ranges from 1.9°C in January to 20°C in July. K is 0.063 and A is equal to 2.1 months. K and A were estimated in the climodiagram.

The first management plans of Navahondona and Palancares were written in 1893 and 1895, respectively. Both forests were then divided into comparments up to 111 hectares in surface, delineated by roads, streams, rocky outcrops and other spatial features. Comparment boundaries have not changed since then. Individual comparments or a number of aggregated ones were established as management units, and for each management unit tactical planning considerations, *i.e. where* and *when* silvicultural treatments would be applied, were defined. The two study forests were first put under the shelterwood method, with a shelter-phase of 20 years and a rotation period of 100 years in Palancares and 120 years in Navahondona. Due to the difficulties in achieving successful natural regeneration, an uneven-aged system began to be applied in Navahondona around the 1920's and, finally, an ideal reverse-J diameter distribution was defined as the target of management in 1944. The cutting cycle was established in 15 years and the maximum residual diameter at breast height (DBH) in 50 cm. The ratio between the number of trees in one diameter class to the number of trees in the next larger class (q) was set in 1.7 for 10 cm width diameter classes. The shelterwood method has remained in Palancares ever since. Therefore, Navahondona served as a model of the selection method and Palancares as a model of the shelterwood method, but silvicultural treatments were not replicated within each of the two study forests.

Although management plans should be ideally revised every 10 years, different types of problems (Civil War, budget restrictions, etc) resulted in Navahondona management plan being revised six times to present; 10 times in the case of Palancares. Until 1980s, every revision was acomplished by a forest inventory independently done for each comparment. Inventories were carried out by the complete enumeration of the standing trees. Specifically, surveyors tallied all trees with a diameter at breast height (DBH, 1.30 m height) equal to or larger than 20 cm in classes of 10 cm. Inventories from Navahondona include numerical data of different pine (*Pinus nigra*, *P. pinaster* and *P. halepensis*) and oak species (*Quercus ilex* and *Q. faginea*, although data belonging to these species are normally grouped together). On the contrary, inventories from Palancares only include data for *Pinus nigra*, because the presence of other tree species is negligible there.

Data set and analysis

In order to answer questions (1) and (2), this research was restricted to those comparments where *Pinus nigra* was the dominant tree species and there was a complete set of data, *i.e.* the whole of Palancares (4,848 ha; 85 comparments) and part of Navahondona (4,332 ha; 77 comparments). We used data from forest inventories carried out in 1920, 1944, 1959, 1967 and 1979 in Navahondona, and from forest inventories carried out in 1906, 1915, 1928, 1942, 1952, 1967 and 1975 in Palancares. This represents a comparable period of time, during which forest inventories were carried out by the complete enumeration of the standing trees. Theoretically, there is no sampling error in the inventories carried out by the complete enumeration of the standing trees. For this reason, we did not analyse data from the most recent forest inventories, carried out by sampling methods, although they were considered during the writing of results. We made this decision on the basis that, in sampling inventory methods, there is a maximum error allowed at the management unit level (15%), but error remains unknown at the comparment level. Records from the 1890's forest inventories were either considered, because they were thought to be insufficiently accurate.

We evaluated the general effect of management plans in both forests by observing changes in the number of merchantable (DBH ≥ 20 cm) and non-merchantable trees over the study period. Diversity profiles of *Pinus nigra* basal area were constructed to follow changes in horizontal diameter class diversity in order to search for the effects of management in the frequency distribution of DBH classes over time. The overall basal area for each DBH class was rank to complete a *right tail-sum* by calculating sucessively the relative abundance of the less frequent DBH class, then the relative abundance of the two less frequent DBH classes considered together and so on, as explained in Solomon and Gove (1999).

The number of large trees within the species *Pinus nigra* was followed across forest inventories. We determined 50 cm as the DBH threshold above which *Pinus nigra* individuals would be considered large trees, 50 cm DBH representing the averaged size of mature trees that begin to develop the architectural elements found in veteran trees, such as decurrent branches and maximun height (Tíscar, 2004).

The proportion of basal area (the whole basal area within each comparment as data were not transformed to m^2 per hectare) by DBH classes was used to compute the Shannon's index (equation [1]) as many times as comparments were within each studied forest. The calculation was then repeated for species, and the two indices were then averaged to maintain a scale similar to the original Shannon's index (the post-hoc method of Staudhammer and LeMay, 2001). We also followed the evolution of the basal area of *Pinus pinaster P. halepensis* and *Quercus* sps. during the study period.

Differences between inventories were search by one-way analysis of variance for each forest separately. Values of the Shannon's indices were not transformed, because analysis of variance are robust to departures from the assumptions of normality and homocedasticity, if data are balanced (*i.e.* sizes of samples are all made the same) and samples are large (Underwood, 1997). Otherwise, non-parametric analysis were applied.

In order to answer question (3), a partial redundancy analysis was conducted to assess the degree of relationship between current structure and the history of silvicultural methods applied and/or environmental conditions (Zuur *et al.*, 2007). Structural and environmental variables were obtained from 22 inventory plots of the Third Spanish National Forest Inventory (3SNFI), located within the study areas of Navahondona and Palancares. Detailed information about the SNFI methods can be found in Bravo *et al.* (2003).

Shannon's index (Hdbh) and the number of large trees (LTno), as explained earlier, and the maximum DBH (Mdbh) were included in the redundancy analysis (RDA) as response variables. The explanatory variables were divided into two groups: environmental variables that included elevation (ele), slope (slo), aspect (asp) and rockiness (roc), and management variables, which included the silvicultural method applied (*SMA*: selection or shelterwood as a binary variable) and whether harvest operations had been carried out recently (*RHO*: yes or no as a binary variable).

Variance partitioning was performed to determine the total variance explained, the pure environmental effect, the pure management effect, the shared effect and the amount of residual 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 and used the sum of all canonical eigenvalues to assess how well a specific selection of explanatory variables explains the variance considering the marginal effects. Throughout the paper, values are means ± standard deviations.

Results

Although Navahondona and Palancares were harvested continuously during the studied period, both forests increased their growing stock. Thus, the number of merchantable trees (DBH ≥ 20 cm) increased over the studied period at both forests, from 466,776 stems to 493,555 stems in Palancares and from 293,449 stems to 350,819 stems in Navahondona.

The number of non-merchantable trees, *i.e.* trees between 10 and 20 cm in diameter, declined in Palancares from a maximum of 1,318,060 stems in 1928 (272 per ha) to 748,781 trees in 1975 (154 per ha) and to a minimum of 461,068 trees at present (95 per ha). The number of non-merchantable *Pinus nigra* trees also declined in Navahondona, from a maximum 302,557 stems in 1967 (70 per ha) to 163,055 stems in 1979 (38 per ha) and to about 125,000 stems at present (29 trees per ha). The number of non-merchantable trees is obviously related with the success of regeneration. In this respect, the management plans written for Palancares have frequently shown concern about the silvicultural method applied, while the presence of domestic and wild ungulates has been quoted by foresters as the main limiting factor of *Pinus nigra* regeneration in Navahondona. Nevertheless, the implementation of management practices towards the end of the eighteenth century helped the establishment of new trees in both forests.

Diversity profiles showed the presence of bigger *Pinus nigra* trees in Navahondona, and a constant decline in the proportion of large trees in both forests (Fig. 2). The number of large black pines was reduced by half in Palancares, from 28,061 stems (6 per ha) to 11,484 stems (2.4 per ha) between 1906 and 1975. The number of large *Pinus nigra* also decreased in Navahondona, from 54,513 trees in 1920 (12.6 per ha) to 31,713 trees in 1979 (7.3 per ha).

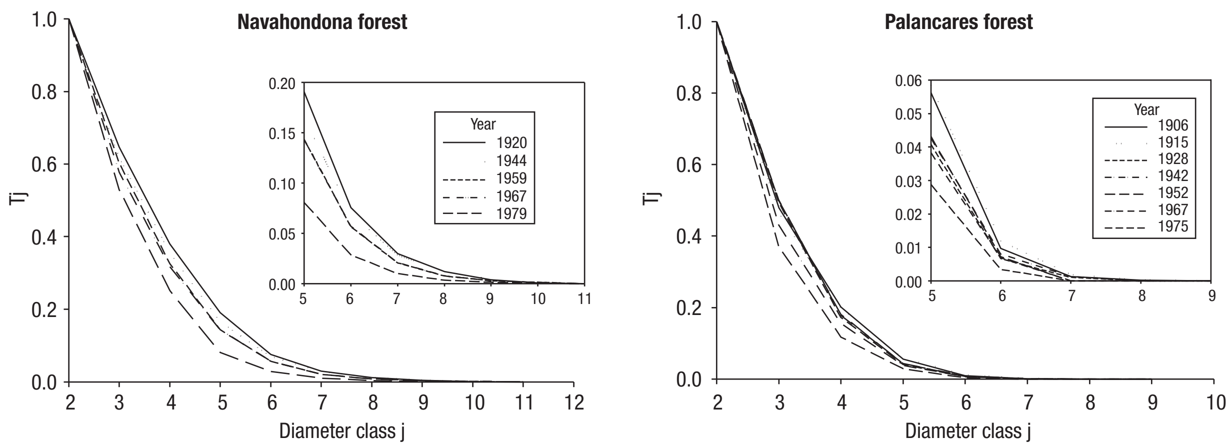

Figure 2. Right tail-sums (T_j) diversity profiles of basal area for the two study forests.

Shannon's index calculated for DBH classes differed between forest inventories in both Palancares ($F_{6, 588} = 18.24$; $p < 0.0001$) and Navahondona ($F_{4, 380} = 7$; $p < 0.0001$). In Palancares, mean values of the Shannon's index declined gradually from an initial value of 1.354 in the 1920 forest inventory to a final value of 1.032 in 1975. Mean values of Shannon's index for the successive forest inventories of Navahondona were 1.857, 1.747, 1.763, 1.790 and 1.670 (Fig. 3). This shows that structural diversity was higher in Navahondona than in Palancares both at the beginning (Mann-Whitney U test; U = 366; $p < 0.000$) and at the end of the study period (Mann-Whitney U test; U = 6,261; $p < 0.000$). As a percentage, the mean reduction of Shannon's indices was significantly higher in Palancares than in Navahondona between the first and last forest inventories (–18.98 ± 11.63% *vs.* –10.13 ± 11.63%; Mann-Whitney U Test, U > 2,508, $p < 0.05$).

Shannon's index calculated for tree species (only for Navahondona) did not differ between forest inventories ($F_{4,380} = 0.13$; $p > 0.10$), although basal area increased for the three species recorded in forest inventories: *Pinus nigra*, *P. pinaster* and *Quercus* sps. (*Quercus ilex* plus *Q. faginea*); *Pinus halepensis* has gradually become part of the growing stock of Navahondona, but the actual contribution of the species is still negligible in terms of basal area. *Pinus pinaster* currently represents 4.5% of the overall basal area in the comparments considered. *Quercus* basal area decreased between 1920 and 1944, despite the fact that there were more comparments containing *Quercus* species in 1944 (28 *vs.* 64). This happened because *Quercus* stands functioned as coppice woodlands and were heavily harvested during the time of the First World War. The sprouts of these stands were still too small to be counted in 1920, but had grown and were recorded in the forest inventory of 1944. From this year onwards, *Quercus* basal area only increased slightly due to a lack of selvicultural treatments (it is only very recently that *Quercus* stands are being coppiced with the aim of producing standars). On the other hand, *Pinus nigra* is almost the only tree species present in Palancares (*Quercus ilex*, *Q. faginea* and *Juniperus thurifera* account for less that 3% of the current standing volume according to the most recent forest inventory). The average of the Shannon's indices calculated for species and DBH classes (post-hoc method) did not differ between forest inventories ($F_{4,380} = 18.24$; $p > 0.05$).

According to data from 3SNFI plots and compared to Palancares, Navahondona attains the highest mean values for the following structural and environmental variables at present: Shannon's index for DBH classes (1.83 *vs.* 1.12), number of large trees (14.6 *vs.* 0.3 stems per hectare), maximum DBH (65 *vs.* 33 cm), elevation (1415 *vs.* 1232 m a.s.l.), slope (25 *vs.* 5 degrees) and rockiness (~50% *vs.* ~25%), all the differences being significant (Mann-Whitney U test, U > 9, $p < 0.01$ in all the cases). Aspect did not differ between forests. Despite these differences, the pure environmental effect accounted for 4.8% of the total variance observed in the variables used to describe stand structure, whilst the variance accounted for management variables was 8.4%, as shown in results of various RDA and partial RDA (Table 1). The variance partitioning is presented in Table 2. The shared amount of variation was 20.2%, *i.e.* the information that can not be distinguished due to collinearity between the two groups of explanatory variables. Variance decomposition

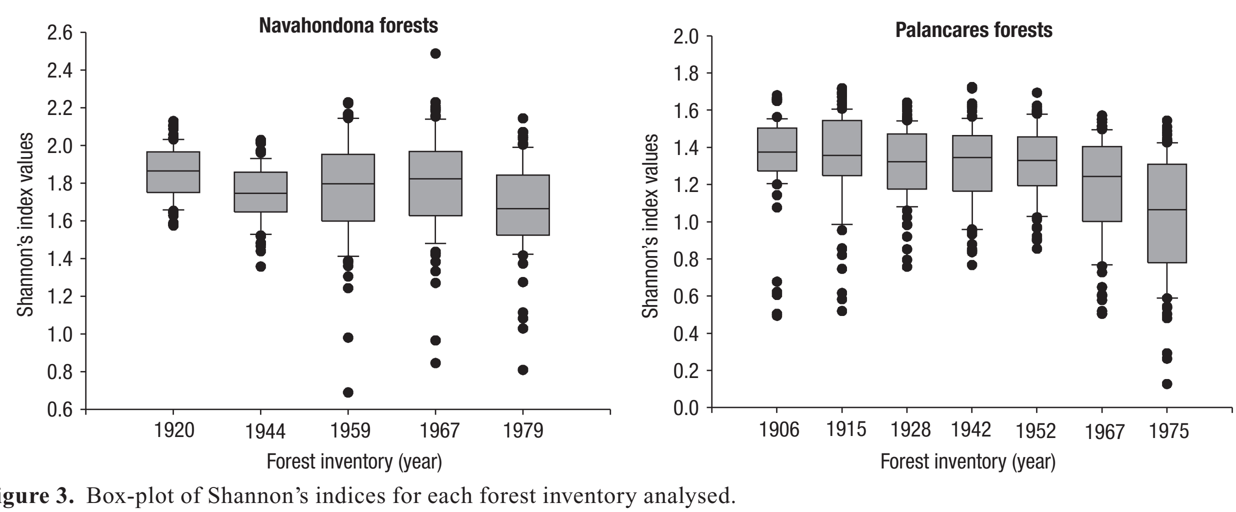

Figure 3. Box-plot of Shannon's indices for each forest inventory analysed.

Table 1. Results of various RDA and partial RDA for environmental and management explanatory variables

Step	Explanatory variables	Explained variance (%)
1	Environmental and management variables	33.4
2	Environmental variables	24.9
3	Management variables	28.6
4	Environmental variables with management as covariable	4.8
5	Management with environmental variables as covariable	8.4

Total inertia is 1.628.

Table 2. Variance decomposition showing the effects of environmental and management variables

Component	Explanatory variables	Explained variance (%)
A	Management variables	8.4
B	Environmental variables	4.8
C	Shared (3-5)	20.2
D	Residual	66.7
Total		100

Components A and B are equal to the explained variances in steps 5 and 4 of Table 1. C is equal to variance in step 3 minus variance in step 5 of Table 1, and D is calculated as 100 minus the explained variance in step 1 of Table 1.

yielded the effect of management as more important than the effect of environmental variables.

Figure 4 shows the relationships between explanatory variables (environment and management) and response variables (several structural attributes). Slope was positively related to the the diversity for DBH classes, whilst the number of large trees and maximum DBH were related to elevation above sea level and rockiness. The marginal effects of the environmental variables indicated that only slope provides a significant increase in the total sum of eigenvalues when it is included as new variable (Table 3). Similarly, the silvicultural method applied yielded a significant increase in the eigenvalues when it was included in the model (Table 4).

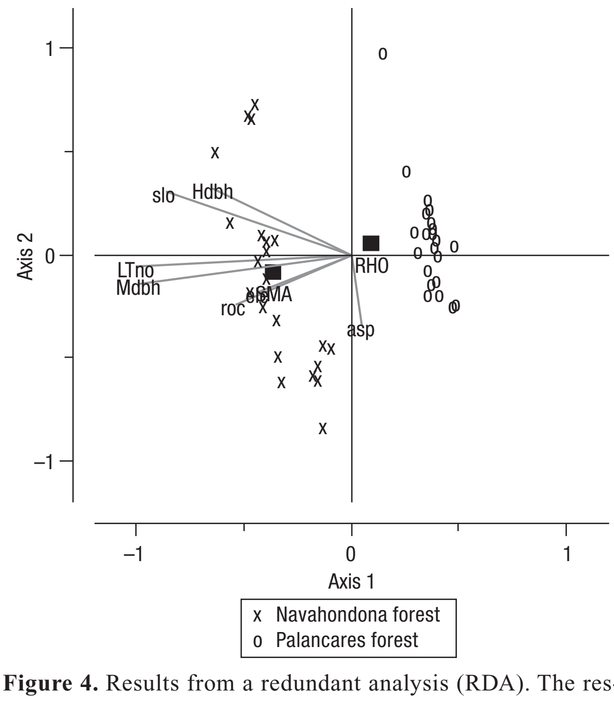

Figure 4. Results from a redundant analysis (RDA). The response variables are represented by thin lines with the following labels: *LTno* (no. of large trees), *Mdbh* (maximum diameter at breast height, dbh) and *Hdbh* (Shannon's index for dbh classes). The quantitative explanatory variables are represented by thick lines with the following labels: *slo* (slope), *ele* (elevation), *roc* (rockiness) and *asp* (aspect). The qualitative explanatory variables are represented by squares with the following labels: *SMA* (silvicultural method applied) and *RHO* (recent harvest operations).

Discussion

Most Spanish forests had been profundly altered and, in many cases, seriously damaged by the time management and silvicultural practices were first implemented in this country. By the end of the 19th century, the two study forests had suffered a long history of overgrazing, fire and illegal felling (Lucas, 2008; Mackay, 1917), and there was great pressure to cut more black pines in order to produce railway sleepers (Araque and Sánchez, 2005). The implementation of planned management in the 1890's brought order to those uncontrolled activities. The proccess of deterioration stopped and forests started to regenerate and the number of pinetrees and the standing volume of timber increased over time (Appendix 1). This situation was repeated in other Spanish forests under public ownership and, as a result, it is generally accepted that planned management improves woodlands (Madrigal, 1994). Here, we argue that management effects on biodiversity should be considered as well and, consequently, we analyse changes in forest composition and structure in two forests with a history of management over the last century. Composition and structure, along with

Table 3. Marginal effects for the environmental variables after the effects of management ones were removed

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	F	p-value
Elevation	0.03	32.97	0.03	2.21	0.106
Slope	0.04	47.09	0.04	2.95	**0.048**
Aspect	0.01	6.86	0.01	0.62	0.593
Rockiness	0.01	7.06	0.01	0.57	0.629

function, are the three attributes that constitute the biodiversity of an area (Noss, 1990).

After more than a century of forest management, Palancares is almost exclusively populated by *Pinus nigra*, the presence of *Quercus ilex*, *Q. faginea* and *Juniperus thurifera* being almost negligible. Similarly, *Pinus pinaster* represents less than 5% of the basal area in Navahondona, and *Quercus* species are even less abundant. Obviously, the distribution of a species occurs within the potential limits established by the environment, and it would be unlikely that *Pinus pinaster* established itself in Palancares or the study comparments of Navahondona, where soils and altitude would be unsuitable for this species. Aditionally, *Pinus nigra* is more shade tolerant and eventually establishes beneath the *Pinus pinaster* trees that first colonized the open spaces, so *Pinus nigra* tends to substitute *Pinus pinaster* in the contact zone of both species by a process of natural succession. These results demostrate that *Pinus nigra* exhibits adaptive capacity to dominate forest composition within its natural range whatever the silvicultural method applied. However, natural environmental factors can not alone explain why there are so few trees of the *Quercus* species in the study areas (Rivas-Martínez, 1987). Management effects must be then considered as factors which influence the current composition observed in both study forests.

Management plans have constantly considered *Pinus nigra* the principal forest species in both Palancares and Navahondona. This explicitly justified both the felling of *Quercus* species for charcoal production with the ultimate aim of substituting oaks by pinetrees during the first half of the 20^{th} century and, more recently, the absence of appropriate silvicultural treatments to encourage the substitution of pinetrees by oaks in those places where that is the tendency of natural succession (Tíscar, 2003). Consequently, oaks have only survived in specific sites which management plans would eventually accommodate coppice stands.

Management plans select the principal forest species and also determine an adecuate rotation age. This imposes a limit on the maximun age (and size) that a tree can reach in a managed forest, so that few trees, if any, attain large dimensions. The number of large trees reduced gradually in the two study forests as expected, although the density of large trees in Navahondona was three times that found in Palancares. There are at least two reasons that explain that slower reduction of large trees in Navahondona. First, the rotation age was much higher in Navahondona during the study period, *i.e.* 150 years *versus* a rotation age of 100 years in Palancares. Second, uneven-aged silvicultural methods are more flexible and can accommodate extramature trees more easily. However, silvicultural practices do reduce the frequency of large trees (Anderson and Östlund, 2004). For instance, black pines of more than 60 cm in diameter represented 60% of the standing volume of Navahondona just before the first management plan was implemented there in 1893 (Tíscar, 2004).

Old black pines show a distintive arquitecture that might provide biodiversity with types of habitat diffe-

Table 3. Marginal effects for the environmental variables after the effects of management ones were removed

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	F	p-value
SMA	0.13	95.03	0.13	0.48	**0.002**
RHO	0	1.44	0.01	0.01	0.935

rent from those provided by younger trees, but little is known in this respect. As far as we are aware, the only existing information refers to the importance of large black pines as primary sources of deadwood, because the survival of some endangered saproxilic beetles depends on the availability of large snags and logs (Molino, 1996). Navahondona not only exhibited the higher density of large trees by the end of the study period, this forest also comprised the largest stems with some individuals being over 120 cm in diameter (the largest trees in Palancares were 85 cm in diameter). This resulted in a larger number of DBH classes, *i.e.* more «species» to compute equation [1], and in higher values of Shannon's index (Fig. 3). A positive relationship was observed between Shannon's index and slope, but it could be interpreted as an indirect consequence of the silvicultural method (selection) being applied on the steeper slopes from Navahondona to prevent soil erosion (Table 3, Fig. 4). Indeed, the relative contribution of *SMA* almost doubled the contribution of the considered environmental variables in explaining structural variability. Other researchers have also supported the potential of land-use to profoundly change the structure of Mediterranean forests (Linares *et al.*, 2010; Plieninger *et al.*, 2003). These findings were expected, because structure is the outcome of a demographic process and, whilst silvicultural treatments easily determine the mortality rate of tree populations, their influence on seedling establishment is less clear in Mediterranean forests, due to the overwhelming impact of summer drought, and not light availability, on plant recruitment (Tíscar, 2007). It is worth remembering that soils and summer climates are very similar in the two study forests.

The partial RDA method allowed us to disentangle the relative contribution of environmental and management variables, and to overcome the limitation imposed by the fact that silvicultural methods were not replicated within each of the study forests. Yet silvicultural systems are highly variable and the large number of variables and assumptions makes any comparison difficult even within those empirical experiments implemented over relatively small areas (García-Abril *et al.*, 2007; O'Hara and Nagel, 2006). Here, we used many years of data to report results from large areas (thousands of hectares), covering real social and economic restrictions and the natural heterogeneity commonly found in the environmental conditions of Mediterranean mountains (Linares and Tíscar, 2011). This sort of information is acknowledged in adaptive management as a valuable resource (Bravo *et al.*, 2010).

In summary, both the shelterwood method and the selection method were found to decrease structural diversity estimated for DBH classes, although the observed reduction was lower in the forest managed by the selection method. This result was related to a reduction in the number of large trees, due to management prescriptions. Current rotation ages in both study forests (120 years) represent a small fraction of the potential longevity of *Pinus nigra* (500-600 years), and nearly half the frequency of natural fires in Cazorla Mountain Range [229 years (Tíscar and Linares, 2011)]. This appreciation is important, because forests should be manipulated within the limits established by natural disturbance patterns in order to maintain forest biodiversity (Seymour and Hunter, 1999). On the other hand, tree species diversity did not change over the study period, probably because succesional trends need to be encouraged by silvicultural treatments that were not applied.

The selection method usually produces more complex forest structures than those generated by the shelterwood method and, additionally, better resembles the dynamics found in untreated natural areas (Saunders and Wagner, 2008). Similarly, the diameter distributions found in Navahonda should be considered better models in the search for a sustainable silviculture able to maintain biodiversity in *Pinus nigra* stands. Unfortunately, the relationship between species diversity and structural diversity is frequently found to be weak, at least for plant communities (Osorio *et al.*, 2009; Neumann and Starlinger, 2001). The presence of correlations between those variables appears to be a field for future research in *Pinus nigra* forests.

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Appendix 1. Summary of inventory variables recorded for every forest and inventory date over the study period

No.	Palancares forest						Navahondona forest					
	Year	Surface (ha)		No. of trees		Growing stock (m³)	Year	Surface (ha)		No. of trees		Growing stock (m³)
		Total	Forested	dbh < 20 cm	dbh > 20 cm			Total[1]	Forested	dbh < 20 cm	dbh > 20 cm	
1	1906	4,848	4,647	768,142	466,776	22,5275	1920	13,251	10,194	16,229	740,064	624,929
2	1915	4,848	—	837,697	511,890	26,8440	1944	13,251	10,194	10,257	677,141	575,200
3	1928	4,848	—	1,318,060	427,811	22,4906	1959	13,286	10,229	732,132	897,916	768,119
4	1942	4,848	4,409	40,8125	456,779	22,5382	1967	13,266	10,208	792,834	993,490	843,884
5	1952	4,848	4,643	605,613	521,625	32,7899	1979	14,369	11,711	563,112	1,011,800	765,005
6	1967	4,848	4,643	733,507	506,809	29,1677						
7	1975	4,848	4,456	748,781	493,555	25,6375						

[1] Only 4,332 hectares were considered in this research.