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Structure of old-growth and managed stands and growth of old trees in a Mediterranean *Pinus nigra* forest in southern Spain

Pedro A. Tíscar[1]* and Manuel E. Lucas-Borja[2]

[1]*Centro de Capacitación y Experimentación Forestal, C/. Vadillo-Castril s/no., 23470 Cazorla, Spain*
[2]*Science and Technology Department of Agroforestry and Genetics, Higher Technical School of Agricultural and Forest Engineering, University of Castilla-La Mancha, 02071 Albacete, Spain*

*Corresponding author. E-mail: pedroa.tiscar@juntadeandalucia.es

The structural attributes of an old-growth forest remnant of *Pinus nigra* subsp. *salzmannii* located in southern Spain and those from nearby managed forests were compared. Data on environmental and structural variables were collected in 74 forest inventory plots. Significant differences were tested by means of the Mann–Whitney *U*-test. A partial redundancy analysis was conducted to assess the relative contribution of both environmental and management variables in explaining differences in the current structure of old-growth and managed stands. Additionally, 25 trees of different size (range 25.4–98 cm) and age (67–803 years) were cored and dendrochronological methods and bootstrap linear regression were used to study the effects of size and age on tree growth. The old-growth stand exhibited a higher density of large trees (diameter at breast height >50 cm) and greater variability in tree size than managed stands, but lower tree density and, consequently, similar values of stand basal area and volume. Environmental variables accounted for 5.7 per cent of the total variance observed in structural attributes, while the contrasting silvicultural condition (old-growth *vs* managed) accounted for 10.2 per cent. Growth, measured in units of stand basal area, increased continuously with tree size.

Keywords: Mediterranean pinewoods, diameter size distributions, sustainable forestry, dendroecology

Introduction

The maintenance of biological diversity while providing goods and services is a central task of forest management under the current paradigm of sustainable forestry (Seymour and Hunter, 1999). Current approaches for sustainable forest management frequently focus on how forest structure and/or function (natural disturbances) should be managed. Explicitly, they emphasize silvicultural intervention as a cost-effective method to create structural diversity (Franklin *et al.*, 2002; Puettmann *et al.*, 2009; O'Hara, 2014) or to mimic natural disturbance regimes (Moore *et al.*, 1999; Perera *et al.*, 2004). These approaches are designed to maintain the habitats or environmental conditions under which forest-dwelling species evolved and by extension prevent species extinction (Seymour and Hunter, 1999). A consequence of applying these natural-disturbance-based silvicultural approaches is that the 'normal forest model', an idealized forest composed of fully stocked stands with a balanced age-class distribution, no longer constitute a suitable benchmark to guide forest management (Puettmann *et al.*, 2009; Tíscar *et al.*, 2015), but some management guidelines or reference conditions are still needed. Recognizing this, remnant old-growth forests are useful for defining targets for structural diversity within the context of sustainable forest management (Kuuluvainen *et al.*, 1996; Frelich *et al.*, 2005; Piovesan *et al.*, 2005).

While considerable work has been completed in old-growth forests from the temperate and boreal regions of Europe (Nilsson *et al.*, 2003), there are fewer studies of old-growth forests from the Mediterranean area (Piovesan *et al.*, 2005; Firm *et al.*, 2009; Keren *et al.*, 2014). In this study, we describe structure and tree growth in an old-growth forest remnant from southeast Spain that is dominated by *Pinus nigra* Arn. subsp. *salzmannii* Dunal (Franco) (*Pinus nigra* hereafter). *Pinus nigra* is native to the calcareous Mediterranean mountains of eastern Spain and southern France. This remnant old-growth stand is unusual, because Mediterranean forests have typically been affected by a long history of anthropogenic alteration (Carrión *et al.*, 2001), and Spanish forests of *P. nigra* were intensively harvested to provide railway-sleepers during the first half of the twentieth century (Tíscar *et al.*, 2011). In fact, studies of *P. nigra* old-growth forests are currently inexistent, although *P. nigra* can live for several centuries and it is still possible to locate forest sites in which very old individuals are present (Fulé *et al.*, 2008).

A description of stand structure is important for the understanding and management of forest ecosystems. Structural attributes constitute an adequate surrogate of forest biodiversity (Franklin *et al.*, 2002; McElhinny *et al.*, 2005), and they are readily measured and easy to manipulate to achieve management objectives, such as resource production (e.g. timber) or service provision

(e.g. carbon sequestration and biodiversity conservation). A number of studies have shown that managed forests have less structural complexity compared with primeval forests (Kuuluvai-nen *et al.*, 1996; Fujimori, 2001). However, it is unclear to what extent forest management could have affected structure in forests from the Mediterranean mountains, since forests had already been profoundly altered by the time silvicultural techniques were first implemented in the area (Tíscar *et al.*, 2011). A description of forest structure can also help to reconstruct stand dynamics and past disturbance regimes. The structural attributes of a site are, in fact, the result of demographic processes triggered by disturbances that kill the standing trees and provide conditions for the establishment of seedlings. Therefore, old-growth forests can offer insights into the prevalent natural disturbance regime in an area and thus provide an indication as to the most suitable silvicultural methods to apply (Franklin *et al.*, 2002).

Natural disturbances rarely eliminate all trees from a stand (Franklin *et al.*, 2002; O'Hara, 2014). Also, rotation periods usually represent a small fraction of the potential life-span of the harvested species. Thus, long rotations and structural retention at harvest are important elements of silvicultural approaches purporting sustainability (Curtis, 1997; Lindenmayer *et al.*, 2012a), but some concerns might arise.

Yield tables have consistently shown that the accumulation of woody biomass slows as even-aged stands age (Ryan *et al.*, 1997). As a result, long rotations and structural retention may represent an economic loss for forest owners (Fujimori, 2001). Previous research has revealed that older trees attain lower growth efficiency (wood production per unit of leaf area) compared with adjacent younger trees in some pine species (Ryan *et al.*, 1997), although mass growth rates tend to increase continuously as pine trees increase in size and age for most species (Stephenson *et al.*, 2014). An additional matter of concern is disentangling the effects of size and age on tree growth since older trees tend to be larger (Peñuelas, 2005). Here, we took advantage of the old-growth study stand to measure tree performance in very old (and large) trees. This age class of trees is seldom included in ecological studies, because it is absent or rare in contemporary forest stands.

In summary, our object was to gain insights into the structure and functioning of a Mediterranean old-growth forest stand, which could subsequently guide silvicultural practice in managed forests. In particular, we addressed the following questions: (1) What are the structural characteristics of the study old-growth stand? (2) How does it compare with managed contemporary stands of *P. nigra*? (3) What is the net basal area increment of larger and older *P. nigra* trees compared with smaller, younger individuals?

Material and methods

Study area

The study was conducted in 13 compartments of the 'Poyo de Santo Domingo' forest (PSD-forest hereafter), located at the southern limit of Cazorla, Segura and Las Villas Natural Park (Jaén province, SE Spain). The area forms part of an abrupt calcareous mountain. The predominant soils are rendzinas and the climate is Mediterranean with wet, cold winters and hot, dry summers. The mean annual rainfall is 1333 mm and the mean annual temperature is 11.46°C ('Cañada de las Fuentes' Meteorological Station, 37° 50′ N, 25″ 2° 58′ W; 1474 m.a.s.l.). Various pollen stratigraphies indicate that the region has been continuously wooded by *P. nigra*

since the beginning of the Holocene (Carrión *et al.*, 2001). Currently, the most abundant tree species in the PSD-forest are (in decreasing order of abundance): *P. nigra, Quercus ilex, Pinus halepensis, Pinus pinaster* and *Quercus faginea*. See Gómez-Mercado (2011) for a more detailed description of vegetation in the study area.

The area of the old-growth stand (ca. 45 ha) approximately coincided with one of the PSD-forest compartments. It contains an unusually high number of very large old trees, and all age-classes are present (Creus, 1998). The site was not accessible by road until the late 1950s and, then, timber companies realized that logs would be too large to process. As a result, the stand escaped the extensive logging activity that affected the PSD-forest during the twentieth century. Yet a few cut stumps are present as some trees were felled for xylometric studies and pest prevention in the 1970s (Carrasco and Badillo, 2004). *Pinus nigra* and some scattered individuals of *Acer opalus* subsp. *grantensis* are the only tree species present. Tree regeneration occurs naturally. Grazing by domestic livestock has not been allowed since 1893, although the site has been occasionally grazed since then, and wild ungulates are present. Among this guild of animals, there are two exotic species, introduced in the 1950s: wild sheep (*Ovis musimon*) and fallow deer (*Dama dama*), that exert a small amount of herbivore pressure on *P. nigra* saplings (García-González and Cuartas, 1992). To this extent, the stand would conform with typical old-growth criteria (Peterken, 1996; Wirth *et al.*, 2009).

The remaining 12 PSD-forest compartments (ca. 575 ha) were included in the study because their environmental conditions resembled those from the old-growth forest stand, and because they were representative of the most intensively harvested *P. nigra*-dominated area within the PSD forest. No less than 37 789 trees (58 213 m^3) were cut in these forest compartments (managed stands hereafter) between 1899 and 1990. During most of this period, the PSD-forest was harvested applying uneven-aged silvicultural methods. The first management plan for the PSD-forest was written in 1893 (Carrasco and Badillo, 2004).

Dataset and the analyses of structure

We used plots from the PSD-forest inventory carried out in 2002 (Carrasco and Badillo, 2004) to compile a set of data from which we could study forest structure in both the old-growth stand and the contemporary managed stands. The forest inventory consisted of 13 m radius circular plots systematically distributed on a square grid of 150 m throughout the PSD-forest. For every plot, we noted the value of three environmental variables: elevation (m a.s.l.), aspect (North: 376–75^g, East: 76–175^g, South: 176–275^g, West: 276–375^g) and slope (1: 0–5°, 2: 6–16°, 3: 17–26°, 4: 26–45°, 5: >45°) as coded in the PSD-forest inventory. The aspect categories south, west, east and north were then given, respectively, the values 1, 2, 3 and 4 in the statistical analysis (see later). In doing this, aspect categories followed a gradient from warmer to cooler microclimate conditions, which can have a potential influence on forest development. These three variables are good descriptors of site productivity, since slope is correlated with soil properties, and altitude and aspect determine microclimate differences between sites. We also noted the identity and diameter at breast height (1.30 m above the base, d.b.h.) of adult trees (d.b.h. ≥2.5 cm) in the plot.

A total of 74 plots were included in the study: the 20 plots within the limits of the old-growth stand and 54 plots from the managed stands in which *P. nigra* occurred as the dominant tree species (basal area >98 per cent). Discarded plots from managed stands included mixed-forests of pine and oak species (*Q. ilex* and *Q. faginea*) and, consequently, attained structural attributes that differed from those observed in the more extended pure managed stands of *P. nigra*. The following structural variables were computed for each plot: mean d.b.h. in centimetres (mdbh), maximum d.b.h. in centimetres (Mdbh), coefficient of variation of tree diameter (CV), density expressed as trees per hectare (den), stand basal area expressed as square metre per hectare (Sba), volume expressed as cubic metre per hectare (vol), and density of large trees expressed as trees per hectare (Ltno). Volume was calculated using the formulae

provided by the 2002 PSD-forest inventory (Carrasco and Badillo, 2004). The d.b.h. threshold above which *P. nigra* individuals were considered large trees was established at 50 cm, since management plans for the study area fixed this value as the maximum residual d.b.h. (equivalent to a rotation period of 150 years). We used the aforementioned structural variables to describe forest structure. The significance of differences between old-growth and managed stands for each structural and environmental variable was tested by means of the Mann–Whitney *U*-test.

We also conducted a partial redundancy analysis (RDA) to assess the degree of relationship between current structure and the presence of management and/or environmental conditions in the old-growth and managed stands (Zuur *et al.*, 2007). The aforementioned structural variables were included in the RDA as response variables. The set of explanatory variables included three environmental variables (altitude, aspect and slope) and one management variable (old-growth *vs* managed stands), expressed as a binary variable with a value of 1 for managed stands and 0 for old-growth ones.

Variance partitioning was performed to determine the total variance explained when considering the pure environmental effect, the pure management effect, the shared effect and the amount of residual variation. Finally, to test which of the single explanatory variables was 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 explained the variance considering the marginal effects (see Zuur *et al.*, 2007). RDA was performed with the Brodgar statistical package version 2.4.1 (Highland Statistics, Newburgh, UK).

Dendrochronological analysis

The old-growth stand was searched thoroughly for the presence of fire-scars at the base of tree trunks as indicative of past fire events. We then compiled a dendrochronological dataset, reutilizing 25 cores of *P. nigra* that had been collected in the stand for previous research studies (see Tiscar, 2002 and Linares and Tiscar, 2010). Trees included in the sample exhibited a wide range of diameters (25.4–98 cm) and, presumably, ages. Tree cores (one core per tree) were extracted parallel to elevation contours at breast height, using an increment borer. The stem circumference and bark thickness of each sampled tree were measured at breast height. All of the sample cores reached the pith. Extracted cores were mounted and sanded, measured on a Velmex 'TA' System device to the nearest 0.01 mm, and cross-dated using standard dendrochronological methods (Cook and Kairiukstis, 1990).

We used a forest management approach to compute a periodic annual increment of basal area (PBAI) for the period 1991–2000, the most recent

decade common to all the samples. PBAI was calculated for the stem inside bark of each tree, after correcting ring width measurements for the possible presence of eccentricity using the proportional diameter-reconstruction method explained in Bakker (2005). The relationship between PBAI and diameter inside bark and between PBAI and tree age were analysed by means of simple regressions. The significance of the regression coefficients was tested by bootstrapping (bias-corrected accelerated percentile intervals or BCa) using the *boot* library in R (R Core Team, 2014). The coefficients were considered significant if their 95 per cent confidence interval did not include zero.
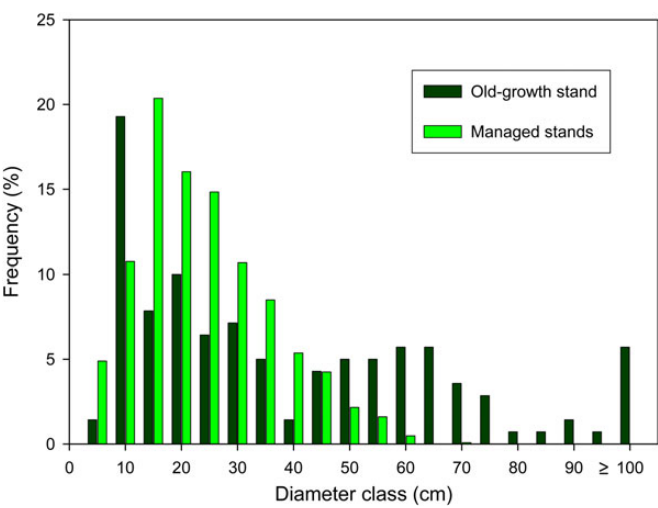
Results

Forest structure

Structural characteristics of the old-growth stand were, in general, significantly different from those found in managed forests (Table 1). The old-growth stand exhibited a higher mean d.b.h., but a non-significant (at $P < 0.005$ after Bonferroni's corrections for 10 variables) higher coefficient of variation for tree diameter indicating similar tree size variability at the plot level. However, the old-growth site showed a much wider range of diameter classes at the stand level (Figure 1). The old-growth stand also exhibited a higher density of large trees and greater tree size (indicated by the mean value of the maximum d.b.h. in each plot). Thus, large trees comprised 32.9 per cent of all inventoried trees in the old-growth stand, while the fraction of large trees was 8.8 per cent in managed stands. In contrast, overall tree density was much lower in the old-growth stand, resulting in non-significant differences in stand basal area and volume between the old-growth and managed stands (Table 1).

The environmental variables altitude and aspect were significantly different between the old-growth and managed stands (at $P < 0.005$ after Bonferroni's corrections for 10 variables), but no significant difference was detected for the variable slope (Table 1). Despite these environmental differences, the pure environmental effect accounted for 5.7 per cent of the total variance, while the variance accounted for by management variable was 10.2 per cent (Table 2). The shared amount of variation, the information that cannot be distinguished due to collinearity between the environmental and management variables, was 17.4 per cent. Variance decomposition suggested that the effect of

Table 1 Mean values and standard deviations of the abiotic and stand-structural variables measured in the studied *P. nigra* stands

Variable	Old-growth stand ($n = 20$)	Managed stands ($n = 54$)	*P*-value
Aspect (S: 1, W: 2, E: 3, N: 4)	1.25 ± 0.44	2.65 ± 0.95	**<0.00001**
Slope	2.35 ± 0.88	3.06 ± 1.00	0.00826
Altitude (m.a.s.l.)	1830 ± 31	1480 ± 98	**<0.00001**
Mean d.b.h. (cm)	46.27 ± 15.86	25.66 ± 7.81	**<0.00001**
Mean maximun d.b.h. (cm)	84.71 ± 17.55	43.87 ± 9.67	**<0.00001**
Coefficient of variation of tree diameter	0.50 ± 0.26	0.38 ± 0.16	0.03523
Density (trees ha^{-1})	120.24 ± 76.66	403.30 ± 270.78	**<0.00001**
Large tree density (trees ha^{-1})	39.59 ± 17.55	11.51 ± 21.78	**<0.00001**
Stand basal area (m^2 ha^{-1})	20.82 ± 9.06	20.46 ± 10.67	0.81421
Tree volume (m^3 ha^{-1})	127.21 ± 51.01	121.59 ± 75.52	0.36775

Number of plots and units are shown between parentheses. Significant differences at $P < 0.005$ after Bonferroni's corrections for 10 variables are marked in bold.

Figure 1 Diameter size distributions for the old-growth and managed stands in the study forest.

Table 2 Results of various RDA and partial RDA analysis for environmental and management (unmanaged old-growth *vs* managed stands) explanatory variables

Step	Explanatory variables	Explained variance (%)
1	Environmental and management variables	33.4
2	Environmental variables	23.1
3	Management variable	27.6
4	Environmental variables with management as covariable	5.7
5	Management with environmental variables as covariable	10.2

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

Component	Explanatory variables	Explained variance (%)
A	Management variable	10.2
B	Environmental variables	5.7
C	Shared (3 – 5)	17.4
D	Residual	66.7
Total		100

Components A and B are equal to the explained variances in steps 5 and 4 of Table 2. C is equal to variance in step 3 minus variance in step 5 of Table 2, and D is calculated as 100 minus the explained variance in step 1 of Table 2.

management was more important than the effect of environmental variables (Table 3). The sum of all canonical eigenvalues from the RDA was 0.27 and the total inertia or variance was 1. Hence, the explanatory variables explained 27 per cent of variance. From this 27 per cent, the first two axes explained 98.7 per cent (Figure 2).
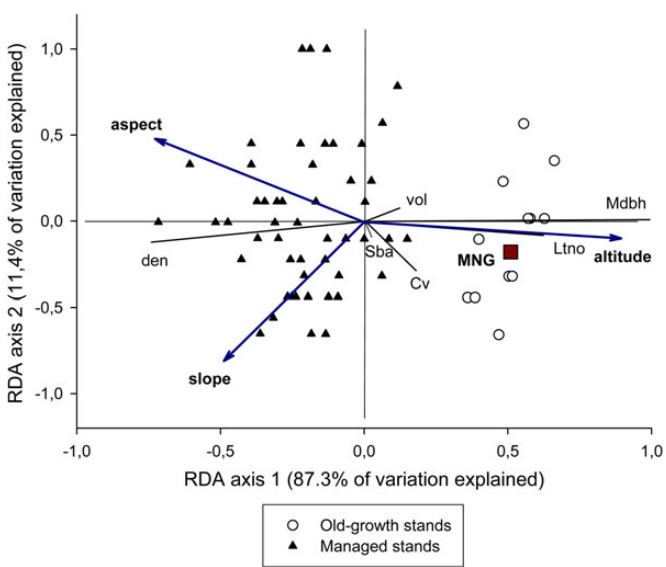
Figure 2 Results from a redundant analysis (RDA). The response variables are represented by thin lines with the following labels: Sba (stand basal area), vol (tree volume), den (tree density), LTno (density of large trees), Mdbh (mean maximum diameter at breast height), and coefficient of variation of tree diameter (CV). The quantitative explanatory variables are represented by thick arrow lines with the following labels: slope, altitude and aspect. The qualitative explanatory variable is represented by a square with the following label: MNG (unmanaged old-growth *vs* managed stands).

Altitude above sea level was positively related to maximum d.b.h. and to the density of large trees (d.b.h. $\geq$ 50 cm), while tree density was related to aspect and slope (Figure 2). The marginal effects of the environmental variables indicated that altitude and slope provide marginally significant increases in the total sum of eigenvalues when they were included as new variables (Table 4). The presence of silvicultural management yielded a significant increase in the eigenvalues when it was included in the model (conditional effects = 0.10, F = 0.001, P < 0.01).

Pinus nigra growth

Cored trees exhibited a large variability in size and age: d.b.h. ranged from 25.4 to 98 cm and tree age varied from 67 to 803 years. Age and d.b.h. were strongly and positively correlated ($R_{Spearman} = 0.775$; $n = 25$; $P < 0.0001$), revealing a multi-aged distribution of forest structure. PBAI was 137.3 ± 119 cm^2 (mean $\pm$ SD) for the period 1991 – 2000, ranging from 27.6 to 493.2 cm^2 across the 25 sampled trees. Results from the simple regression showed that larger trees tended to produce more basal area [intercept $\pm$ SE = 3.033 $\pm$ 0.036; $\beta \pm$ SE = 0.103 $\pm$ 0.036; 95 per cent BCa = (0.041, 0.188); $R^2 = 0.26$ (Figure 3A)]. However, no relationship was found between BAI and age [intercept $\pm$ SE = 7.817 $\pm$ 1.562; $\beta \pm$ SE = 0.004 $\pm$ 0.004; 95 per cent BCa = [−0.005, 0.011]; $R^2 = 0.02$ (Figure 3B)].
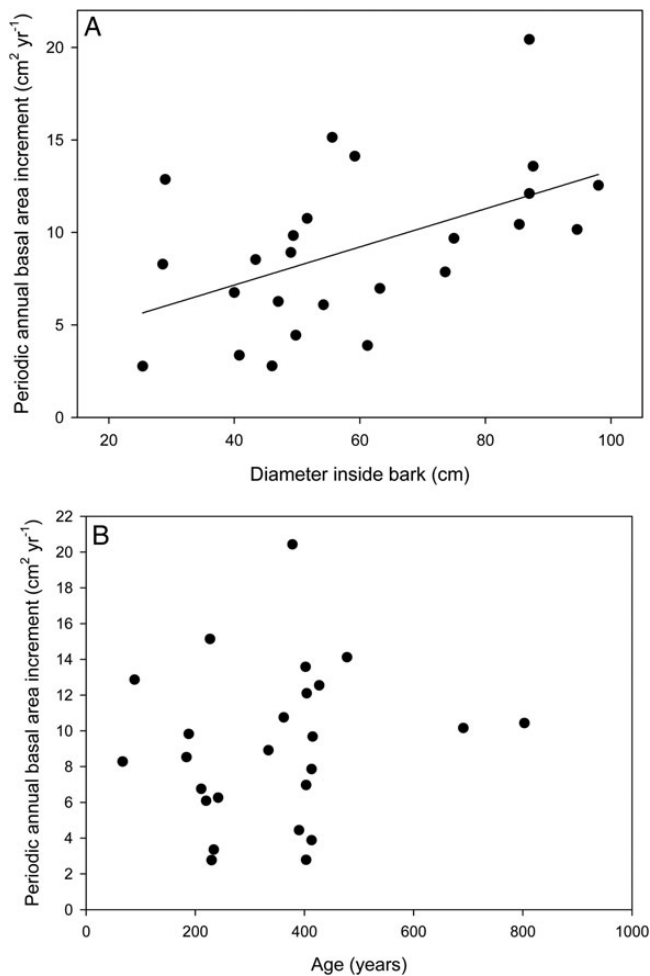
Discussion

Forest structure

Attributes that characterize old-growth forests inevitably vary between forest types, yet all of them share some similarities. The

Table 4 Marginal effects for the environmental variables after the effects of management ones were removed

Variable	Eigenvalue using only one explanatory variable	Eigenvalue as % of sum all eigenvalues using only one explanatory variable	Conditional effects: increase total sum of eigenvalues after including new variable	F	P-value
Altitude	0.02	43.87	0.02	2.023	0.085
Slope	0.02	39.01	0.02	2.309	0.060
Aspect	0.00	3.97	0.00	0.325	0.840

Figure 3 Relationship between the annual basal area increment measured for the 10-year period: 1991–2000 with (A) the diameter inside bark and (B) age of 25 individuals of *P. nigra*. The adjusted regression line is shown ($Y = 3.03 + 0.103\ X$, $P < 0.05$, $R^2 = 0.26$).

In comparison, the managed sites contained smaller trees and exhibited less structural complexity at the stand level. Although these structural differences could be reflecting variability of environmental conditions (Table 1), results from the RDA indicated the greater importance of management. In particular, the relative contribution of silvicultural intervention almost doubled the contribution of environmental features in explaining the current structure of *P. nigra* stands (Table 3). The rotation length specified in management plans imposes a limit on the maximum size (and age) that a tree can reach in a managed forest, so few trees, if any, attain larger dimensions (i.e. 50 cm d.b.h.). Thus, silvicultural treatments applied in the PSD-forest during the last century, a mixture of the BDq system (q-factor = 1.7, using 10 cm diameter classes; maximum diameter = 50 cm) and the diameter-limit cutting system, aimed at removing trees of over 50 cm d.b.h. from the previously unmanaged forest (Carrasco and Badillo, 2004), would have caused the eventual reduction in the initial large tree density. Indeed, Tíscar *et al*. (2011) showed that such a silvicultural intervention generated the gradual decrease in large tree numbers over the twentieth century in forests from the same natural area.

The application of silvicultural treatments could also explain higher stem density and smaller tree diameters in the managed stands from the PSD-forest. Treatments are designed to harvest mature trees and simultaneously trigger seedling establishment, sometimes with the help of direct seeding and/or tree plantation. Logging based on tree size might also increase the coefficient of variation of tree diameter at the plot level (Angers *et al*., 2005). Additionally, long-term effects of management could certainly have interacted with the environment to favour elevated tree density in the managed stands, since they were located in sites with less harsh conditions than the old-growth stand.

We must also consider the possibility that low tree density could result from the past occurrence of frequent low-intensity fires in the old-growth stand (Fulé *et al*., 2008). Indeed, *P. nigra* exhibits several evolutionary traits that can be interpreted as adaptations to low-intensity surface fires (Tapias *et al*., 2004). However, management records from the PSD-forest show that the site has been unaffected by fire during the last century (Carrasco and Badillo, 2004). In fact, the area is extensively covered by *Juniperus communis* (see Tíscar, 2003), a fire-sensitive shrub species (Thomas *et al*., 2007). The wide range of tree sizes and ages (Figure 1) and the observed absence of fire-scars, both at the base of tree trunks and in the extracted cores, would further confirm this reasoning and would also indicate that the old-growth stand has been unaffected by stand-replacing disturbances for centuries.

Where stand-replacing disturbances are absent or very infrequent, minor or gap-creating disturbances become predominant and multi-aged structures characterize forest stands (Seymour and Hunter, 1999; O'Hara, 2014). Foresters usually describe

most conspicuous structural attributes identified in the old-growth stand studied here were: the wide range of tree sizes, the density of large trees, which accounted for a significant portion of both total stand basal area and total volume, and the sizeable diameters attained by the largest trees. These attributes have frequently been listed as distinctive features of old-growth forests (Peterken, 1996; Wirth *et al*., 2009). In fact, the diameters attained by the largest trees were remarkable (up to 190 cm), considering that the site was located near the altitudinal limit for *P. nigra* (Gómez-Mercado, 2011).

multi-aged stands by means of the frequency distributions of tree diameters, such as the negative exponential distribution or the rotated sigmoid distribution (Wesphal *et al.*, 2006). In this respect, forest structure in the old-growth stand resembled the pattern of a rotated sigmoid distribution (Goff and West, 1975), while the shape of the diameter distribution from managed forests was more similar to a negative exponential distribution (the management target), although exhibiting too low density of saplings (d.b.h. = 5 cm in Figure 1). Poor regeneration of *P. nigra* in present managed stands could be explained by the lack of silvicultural treatments applied in the study area during the last 30 years (Carrasco and Badillo, 2004) and the consequent presence of too dense canopy cover, which prevents seedling establishment (Tíscar, 2007). The density of saplings was equally low in the old-growth stand, where natural regeneration is known to be limited by a number of environmental factors (Tíscar, 2003). In fact, the positive relationship between tree age and size and the several peaks observed in the old-growth diameter distribution (Figure 1) suggest that *P. nigra* does not regenerate continuously in the old-growth stand but in the form of unique events or pulses, whenever recruitment is favoured by a suitable combination of factors (Tíscar, 2007).

Tree growth

A widely held assumption is that growth of individual trees rises, peaks and declines with increasing tree size (Wirth *et al.*, 2009). Although this is probably a generalization from even-aged stands and some studies have reported increased growth efficiency in older age classes from multi-aged forest stands (O'Hara 1996), this assumption has been readily applied in forest management with a great impact on forest structure and biodiversity (Puettmann *et al.*, 2009; Tíscar *et al.*, 2011 and here). However, the present study shows that basal area increases continuously with tree size in *P. nigra* and that large trees (up to d.b.h. = 95 cm inside bark) attain the highest growth rates in the study area (Figure 2a). These results are in agreement with recent research on *P. nigra* growth patterns (Linares and Tíscar, 2010; Stephenson *et al.*, 2014), but refer for the first time to very large and old trees that are normally absent in managed forests and, consequently, are not studied. Although d.b.h. and age were correlated, we found no relationship between BAI and age (Figure 2b). This result was expected, as it is in agreement with studies that specifically tried to disentangle the effects of size and age on tree vitality, concluding that factors mediated by size and not age drive growth rates in older, larger trees (Mencuccini *et al.*, 2005).

Implications for management

Compared with unaltered and unmanaged (old-growth) stands, managed stands from the PSD-forest exhibited a deficit of large trees. Large, old trees play a critical ecological role not provided by younger, smaller trees (Lindenmayer *et al.*, 2012b). However, little is known about *P. nigra* in this respect. As far as we are aware, the only existing information refers to the importance of large pines as a primary source of deadwood, because the survival of some endangered beetles from the study area depends on the availability of large snags and logs (Molino, 1996). The importance of dead wood has long been emphasized in the literature concerning biodiversity conservation and sustainable forestry (Hansen *et al.*, 1991). Unfortunately, the PSD-forest inventory did not measure the volume of dead wood. Girdling and felling medium- to large-sized trees represent the usual operational approaches to increase, respectively, the volume of snags and logs.

The number of large trees could be increased by identifying and retaining legacy trees and by removing competing, low-quality trees adjacent to larger, more vigorous trees. Additionally, extended rotation periods would be needed to increase the number of large trees. Long rotations are biologically reasonable for *P. nigra*, because the species is very long-lived (Creus, 1998) and, as shown in this study, can maintain rapid growth until very advanced ages. Long rotations could also increase timber value and, perhaps, the overall rate of carbon accumulation with positive consequences for the mitigation of climate change (Stephenson *et al.*, 2014). Finally, the multi-aged structure exhibited by the old-growth stand would represent significant information for the implementation of natural-disturbance-based silvicultural approaches in the study forests.

Contribution of the co-authors

P.A.T. conceived the research, obtained the field data, run the data analysis and wrote the manuscript. M.E.L.-B. obtained the field data and wrote the manuscript.

Conflict of interest statement

None declared.

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