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Structure and spatio-temporal dynamics of cedar forests along a management gradient in the Middle Atlas, Morocco

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ABSTRACT

Diameter distribution and temporal and spatial patterns of a *Cedrus atlantica* forest were studied across a management gradient (undisturbed, logged and highly disturbed) in Ifrane National Park, Morocco. Forest structure and regeneration dynamics showed significant differences among management levels. The diameter distribution in undisturbed and logged stands indicated the presence of few young individuals, and a poor regeneration status in highly disturbed stands. Variance in diameter was larger in natural stands compared to managed ones. There was a seedling establishment pulse during the time period between 1910 and 1990 at three sites, but a lack of sapling and juveniles occurred at undisturbed and logged forests in the last century, which might be attributed to competition between *C. atlantica* and *Quercus ilex*. Nevertheless, cedar trees persistently recruited to all forests during the last 50 years, but cedar density was significantly higher in the highly disturbed forest areas. Spatial analysis shows a general trend toward aggregation for all species involved. This pattern was observed among *C. atlantica* trees in undisturbed and highly disturbed stands but was not significant in logged stands. Differences in management may promote variation in stand structure and regeneration dynamics of the subalpine cedar forests along the management gradient in the Middle Atlas, Morocco.

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1. Introduction

Structural attributes of forest stands, size distribution and spatial arrangement of individual trees are increasingly recognized for their theoretical and practical importance in understanding and managing forest ecosystems (Lingua et al., 2008). The species composition, structure, and dynamics of forest stands reflect growth conditions as well as direct and indirect anthropogenic influences, such as management practices, grazing by domestic and wild herbivores, and climate change. The size class structure is the parameter most often manipulated by silvicultural treatments to achieve management objectives and depends on the type, magnitude, severity, and frequency of harvesting and species' life history attributes (Oliver and Larson, 1990).

Silvicultural practices play an important role in shaping the age structure and regeneration dynamics of montane forests (North et al., 2004). For example, opening the canopy in closed forests can enhance the establishment of tree seedlings. Studies addressing stand dynamics provide substantial information on the regeneration and population structures of forests (Ezzahiri and Belghazi, 2000; Parish and Antos, 2004; Lingua et al., 2008) and can be used to infer population responses to forest management (Stephens and Moghaddas, 2007; Puettmann and Ammer, 2007).

Despite the ecological and economic importance of *Cedrus atlantica* in Morocco, little information exists on the structure and dynamics of both undisturbed and managed populations of this species. The largest stands of *C. atlantica* are located in two unequal and highly fragmented areas: the North Moroccan Rif mountains (160 km^2 of forest area) and the Middle and Eastern High Atlas (1160 km^2) (ḾHirit, 1999; Ezzahiri and Belghazi, 2000; ḾHirit and Benzyare, 2006). The distribution of these forests in Morocco strongly depends on climate (Munaut, 1982; M'Hirit, 1982; Till, 1987). The structure and species composition of cedar

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forests in Morocco have been modified by centuries of traditional forest utilization as well as modern management interventions, which have had a serious homogenizing effect on stand structures (Ajbilou et al., 2006). The result of modern silviculture has been a decrease in the variability in size, age, and spatial distributions in comparison with natural stands (Ajbilou et al., 2006).

Assessing and analyzing the age structure and regeneration dynamics of cedar stands are therefore essential for understanding the long-term ecological processes occurring in managed forests. The dynamics driving the recruitment of juveniles into mature populations of *C. atlantica* are regulated by a wide variety of factors, such as erratic seed production, seed predation, herbivore damage, fire frequency, light conditions under the canopy, and climatic variability. However, relating the tree regeneration dynamics in these forests to previous silvicultural treatments has proven difficult (Deil, 1982; Benabid, 1985; Derridj, 1990; Krouchi et al., 2004).

Most studies on the structure of *C. atlantica* forests have focused almost exclusively on how temporal changes relate to extrinsic factors, specifically climate or disturbances such as grazing or fire (Mediouni and Yahi, 1989; Derridj, 1990; Krouchi et al., 2004). No studies on structural dynamics of *C. atlantica* have addressed the spatial structure of establishment and the potential for biotic interactions (inferred from spatial patterns) to mediate the regeneration process. Tree-ring chronologies from managed forests have also improved our understanding of stand dynamics and the coexistence of tree species (Pollmann, 2003). Investigation of tree-ring chronologies coupled with analysis of stand structures, land-use history, climatic data, and ecological attributes of different tree species has proven to be a suitable approach for understanding long-term forest dynamics (Fritts and Swetnam, 1989). Forest management methods inspired by the natural variability of forests and knowledge of natural tree size distributions are also essential for new silvicultural practices (Harvey et al., 2002; Seymour et al., 2002; Candel-Perez et al., 2012).

In this study, we combine analyses of size distributions, temporal patterns, and spatial patterns to gain insight into the size, age structure and regeneration patterns of *C. atlantica* forests in response to three levels of management: i.e., undisturbed, logged and highly disturbed. The Middle Atlas Mountains were selected to represent different situations along a broad gradient of decreasing intensities and durations of forest utilization. Although previous works have modeled the growth and structure of this species at the stand level (Khatouri and Dennis, 1990; Ezzahiri and Belghazi, 2000; Parish and Antos, 2004; Lingua et al., 2008), there is a lack of studies describing the impact of silvicultural practices on the structure and dynamic of cedar forests. The main objective of this study was to compare the stand structures, recruitment history and spatial patterns of cedar forests along a management gradient. Based on this objective, we postulated that (just suggestions) (1) tree density will be higher in highly disturbed stands (2) regeneration structure will vary along the gradient; specifically, seedling and sapling abundance will be higher in logged than undisturbed and highly disturbed stands and (3) clumped patterns will be more often in undisturbed stands than in logged and highly disturbed ones. The results of this study will improve our understanding of the dynamics and management of *C. atlantica* forests in North Africa based on a comprehensive understanding of the structures and regeneration processes in undisturbed and managed forest stands.

2. Materials and methods

2.1. Study area

The study sites were located in the Arzou and Sidi M'Guid forests (33°33′N – 05°14′W) within the 500-km^2 Ifrane National Park (INP),

which is in the Middle Atlas Mountains of central Morocco (Supporting Information; Fig. S1). The area consists of a long, northerly running ridge within a landscape matrix consisting of forest patches, heathlands, and bare soils. The climate is characterized by cool, wet winters and hot, dry summers. Maximum and minimum temperatures recorded between 1975 and 2004 at Ifrane Meteorological Station (1800 m.a.s.l) averaged 17.9 and 9.1 °C in January and 30 and 15.6 °C in August, respectively. Annual precipitation averaged between 700 and 1200 mm, with 7.5% falling between June and August, resulting in late-summer drought. Snow cover usually lasted 15–30 days between November and March (Anonymous, 2007). The dominant soils in *C. atlantica* forests are shallow and calcareous with pH = 6.5–7.9, N/P ratio = 6.89, and high contents of nitrogen ([N] > 100 kg ha^{-1}), phosphorus ([P$_2$O$_5$] = 50–100 kg ha^{-1}) and potassium ([K$_2$O] > 1000 kg ha^{-1}) (Chouraichi, 2009).

C. atlantica forests occur between 1000 and 2800 m.a.s.l. in INP but are rare below 1200 m due to land use pressure. The stands investigated in this study contained emergent individuals of *C. atlantica* sparsely mixed with Quercus *ilex* L. subsp. *ballota* (Desf.) Samp. and, to a lesser extent, Quercus *faginea* Lam., Quercus. *canariensis* Willd., *Acer opalus* Mill., Acer. *monspessulanum* L., *Crataegus laciniata* Ucria., *Fraxinus dimorpha* Coss. & Durieu, and *Juniperus oxycedrus* L. Mean basal area (BA) and stem density (N) of *C. atlantica* in the Ifrane region are 19–21 m^2 ha^{-1} and 167–186 trees ha^{-1}, respectively (Anonymous, 2007). A number of large mammal species inhabit these forests, including the threatened Barbary macaque (*Macaca sylvanus*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and wild boar (*Sus scrofa*).

2.2. Experimental design

Human impacts on forests in INP are spatially heterogeneous and can be classified along a gradient of management intensity ranging from relatively undisturbed forests, regenerating second-growth forests, to highly disturbed areas (Supporting Information; Figs. S2–S5). Undisturbed stands are characterized by relatively low tree removal in the past, absence of recent silvicultural interventions, and abandonment of domestic wood collection. In second-growth forests, scattered old stumps indicate that trees were selectively logged at low intensity until roughly the middle of the 20th century. Although the extent and frequency of logging in these forests is unclear, it is likely that a few moderate to large-sized trees were cut for local use. Highly disturbed areas are characterized by a history of heavy timber extraction, mostly of *C. atlantica*, and domestic goat and sheep grazing. Since Morocco's independence in 1956, the cedar forests of Arzou and Sidi M'Guid have belonged to the Royal Forests. Between 1978 and 2002, these forests were subdivided and subjected to different silvicultural treatments such as shelterwood cutting and regeneration, which are currently characterized by an even-sized stand structure (Anonymous, 2007).

Stands were selected according to the following criteria: (1) at least 10 adult trees were present, (2) the forest patch in which the stand was located was dominated by cedar, (3) reliable information about when the stand was last logged was available, and (4) the site was accessible. In May 2011, twelve 20 × 30 m plots representing the following three levels of management were established in *C. atlantica* stands according to a stratified random design (Table 1; Supporting Information; Figs. S2–S5):

(1) *Undisturbed*: intact stands with minimal silvicultural or human intervention.
(2) *Logged*: areas subjected to periodic silvicultural treatments such as shelterwood felling in small areas.

(3) *Highly disturbed*: areas showing signs of severe, direct human intervention including illegal timber extraction and pruning of mostly of *C. atlantica*, as well as goat and sheep grazing.

In each plot, species were recorded and the height, diameter, and spatial position were measured for all living and dead trees ($n = 468$). The species of all living trees (height > 1.3 m) were identified, and their diameters were measured at breast height (dbh) at 1-cm intervals. Height (h) was measured for adult trees with a dbh > 5 cm to enable reliable estimation of their volume. For age determination and radial growth analysis, one or two sound cores per cedar tree with dbh $\geqslant$ 5.0 cm ($n = 310$) were extracted in the direction parallel to the slope contour using increment borers according to standard dendrochronological field methods (e.g., Grissino-Mayer, 2001). Regenerating individuals were measured in four size classes: seedlings ($h < 50$ cm), short saplings (50 cm $\leqslant h < 130$ cm), tall saplings ($\geqslant 130$ cm and dbh < 5 cm), and juveniles (5 cm $\leqslant$ dbh < 10 cm) (Dobrowolska and Veblen, 2008). Tree crowns were classified as dominant, codominant, or suppressed based on the amount and direction of intercepted light (Smith et al., 1997).

2.2.1. Stand structure

Stand density of adult trees, dbh, height, stand basal area, density of tall saplings and juveniles of *C. atlantica*, *Q. ilex*, *C. laciniata*, and *A. monspessulanum* were compared between the three management types with a one-way ANOVA or Student's *t*-test. Post hoc comparisons between pairs of management types were identified with Tukey's test based on adjusted levels of significance (Sokal and Rohlf, 1995). The assumptions of normality and homogeneity of variance of the residuals were examined using the Kolmogorov–Smirnov and Levene tests, respectively. When the data distribution did not fit a normal curve, the data were subjected to a square root transformation. Null hypotheses were rejected at the $P < 0.05$ level, and all analyses were run with SPSS® (SPSS V.15.02, www.spss.com).

2.2.2. Shapes and properties of size-class distributions

Due to its versatility and simplicity (Bailey and Dell, 1973), the two-parameter Weibull function has been widely used to fit dbh distributions to forest inventory data. When inventorying trees with dbh greater than a minimum diameter, the specified minimum dbh constitutes the truncation point of a left-truncated diameter distribution (Zutter et al., 1986). The two-parameter left-truncated Weibull function has proven more suitable than some other alternative functions for several species growing in the Mediterranean region (Palahí et al., 2007). Furthermore, mixed or complex stand structures may be characterized by bimodal diameter distributions that cannot be accurately represented by means of a single Weibull function. In contrast, the finite mixture models can better describe bimodal or multimodal distributions (Liu et al., 2002). This approach has been used in previous research to model the dbh distributions of uneven-aged stands that do not follow the theoretical J-shaped structure (Zhang et al., 2001). In this study we tested uni- and bimodal, left-truncated and non-truncated two-parameter Weibull functions to model the diameter distributions of *C. atlantica*, *Q. ilex*, *C. laciniata* and *A. monspessulanum* for each site representing a different management intensity gradient. Eq. (1) was used to fit the distribution of *C. atlantica* considering a 5-cm left-truncated bimodal distribution by means of a finite mixture model. No left-truncation was considered when fitting distributions for the other species since the 5 cm minimum dbh was only considered when measuring *C. atlantica* trees. The fitting was carried out using the maximum likelihood method provided by the "mle" R function in the "stats4" package (R Development Core Team, 2011) (e.g., Mehtätalo et al., 2011).

$$f(d) = \rho \frac{\left(\left(\frac{\alpha_1}{\beta_1}\right)\left(\frac{d}{\beta_1}\right)^{\alpha_1-1} e^{\left(-\left(\frac{d}{\beta_1}\right)^{\alpha_1}\right)}\right)}{1 - e^{\left(-\left(\frac{d_{min}}{\beta_1}\right)^{\alpha_1}\right)}}$$
$$+ (1-\rho) \frac{\left(\left(\frac{\alpha_2}{\beta_2}\right)\left(\frac{d}{\beta_2}\right)^{\alpha_2-1} e^{\left(-\left(\frac{d}{\beta_2}\right)^{\alpha_2}\right)}\right)}{1 - e^{\left(-\left(\frac{d_{min}}{\beta_2}\right)^{\alpha_2}\right)}} \tag{1}$$

where α_i and β_i are the shape and scale parameters of each component distribution of the mixture distribution, ρ and $1 - \rho$ determine the relative abundance of the every component as a proportion of

Table 1
Descriptive information about the 12 study plots in Arzou and Sidi M'Guid forests of Ifrane National Park, Morocco.

Management type	Location	Plot	Elevation (m)	Coordinates	Number of tree cores extracted
Undisturbed	Sidi M'Guid	1	1820	N33°19′52.3″ W5°14′29.6″	29
		2	1845	N33°19′50.1″ W5°14′26.5″	14
		3	1847	N33°20′03.3″ W5°14′23.9″	16
		4	1819	N33°19′48″ W5°14′35″	11
Logged	Sidi M'Guid	1	1835	N33°18′59.4″ W5°13′53.2″	9
		2	1809	N33°18′43.1″ W5°13′50.6″	19
		3	1816	N33°18′15.9″ W5°14′30.5″	13
		4	1836	N33°18′49.8″ W5°13′53.6″	23
Highly disturbed	Azrou	1	1820	N33°21′51.4″ W5°13′43.9″	43
		2	1832	N33°20′40.1″ W5°13′52.6″	56
		3	1858	N33°21′44.9″ W5°13′40.9″	51
		4	1851	N33°21′10.9″ W5°13′44.5″	33

the total population, d is diameter at breast height and d_{min} is the left-truncation point.

2.2.3. Dendrochronological methods

To conduct dendrochronological analysis, all tree ring samples were dried and polished in the laboratory with successively finer grits of sandpaper (Yamaguchi, 1991). Visual cross-dating for each sample was conducted under a binocular microscope (Nikon SMZ.1, Japan) and dated samples were measured using a LINTAB measuring system interfaced with the Time Series Analysis Program (TSAP; Frank Rinntech, Heidelberg, Germany, www.rinntech.com) to a precision of 0.001 mm. Visual cross-dating was verified using COFECHA (Grissino-Mayer, 2001), in which the Spearman rank correlation option was selected to diminish the influence of sharp growth reductions caused by insect outbreaks. The age distribution was presented at 10-year intervals.

2.2.4. Spatial patterns of association

To analyze the spatial patterns of association between *C. atlantica* and *Q. ilex*, the overall frequency distributions of species composition, diameter and height were plotted to provide a visual context with which to evaluate the patterns indicated by the statistics. Additionally, the height of each tree was graphed versus its location along the management gradient to allow visual perception of the overall spatial pattern.

To quantify relationships along spatial patterns, Ripley's K-function and the O-ring statistic were applied (Fortin and Dale, 2005). The univariate form of the Ripley's K function was used to describe general patterns of points, while the bivariate form was used to describe the relationships between two different patterns of points, such as between regeneration and adult trees (Fortin and Dale, 2005). Because Ripley's K is a cumulative function and requires care in interpretation, the square-root transformation of $K(d)$, $L(d)$, was used. $L(d)$ has an expected value of 0 if individuals are randomly distributed (Wiegand and Moloney, 2004). The O-ring function, a transformation of the pair correlation function ($g(r)$), was also used. Edge effects were corrected in both analyses using the toroidal correction method (Fortin and Dale, 2005).

Analyses were performed at 0.5-m intervals (the lag distance) from 1 to 10 m. Relationships at shorter distances were emphasized because these are more likely to reflect interactions among neighbors (i.e. clustering or repulsion). Tests were run separately for each of the three levels of management. Confidence boundaries (simulation envelopes) were calculated using a Poisson process model for the number of points in the sample (the bivariate method uses two Poisson process models) (Wiegand and Moloney, 2004). Models were randomly simulated 999 times using a Monte Carlo method, and the minimum and maximum values were considered as the lower and upper 99% confidence boundaries. Values beyond these boundaries were considered significant and plotted as filled dots in the figures (see Sánchez Meador and Moore, 2009). Spatial patterns were evaluated using Programita software (Baddeley and Turner, 2005) and goodness-of-fit (GOF) tests were used to assess the deal with the potential underestimation of type I error (Lawes et al., 2008), p-value associated to GOF are also shown. In plots where the number of individuals was sufficient to analyze intra- and interspecific relationships, a bivariate analysis was carried out. Relationships between adult and juvenile *Q. ilex* and between adults trees of *Q. ilex* and *C. atlantica* were analyzed in undisturbed and antropized stands, while relationships between juvenile and adult *C. atlantica* patterns trees were calculated for all stands. Due to the low number of *Q. ilex* trees per plot, it was only possible to perform spatial analysis of the undisturbed plots.

3. Results

3.1. Stand structure

Among adults, all three management levels were dominated by *C. atlantica* (Table 2). The density of *C. atlantica* individuals (dbh $\geqslant$ 5 cm) ranged from 244 (57% of total tree density) to 622 (99%) trees ha^{-1} among the management levels and was significantly higher in the highly disturbed forest than in the other forest stands ($F = 12.528$; $P = 0.05$). However, the density of *Q. ilex*, the second most abundant species, was significantly higher in the undisturbed stands (161 trees ha^{-1}; 38%) than in the other forest stands ($F = 20.101$; $P = 0.02$). *C. laciniata* and *A. monspessulanum* reached a maximum density of 16.7 trees ha^{-1} in the undisturbed and logged sites, respectively, but were completely absent from the disturbed site. Total basal area of *C. atlantica* ranged from 66.6 to 46.5 m^2 ha^{-1}, while that of *Q. ilex* ranged from 1.8 to 0.01 m^2 ha^{-1}. Across all management types, *C. atlantica* accounted for over 96% of the basal area, *Q. ilex* represented less than 3%, and *C. laciniata* and *A. monspessulanum* contributed a marginal fraction.

C. atlantica seedlings, short saplings, and tall saplings were completely absent from all three management levels. *C. atlantica* juveniles were least dense (16.7 tree ha^{-1}) in logged stands, but differences were not significant ($F = 0.130$; $P = 0.880$). Density of *Q. ilex* tall saplings in the undisturbed forest (27.8 ha^{-1}) was more than twice that in the other forest stands, although this difference was not significant ($F = 1.565$; $P = 0.279$, Students t-test) (Table 2). The undisturbed forest was also the site where the juvenile density of *Q. ilex* was highest (155 trees ha^{-1}) ($F = 9.955$; $P = 0.012$). Densities of *C. laciniata* tall saplings and juveniles were more abundant in undisturbed and logged forests than highly disturbed forests, with significant differences being detected among management levels for sapling ($F = 6.400$; $P = 0.065$, Students t-test).

The mean dbh of *C. atlantica* ranged from 49.0 cm (logged) to 36.6 cm (highly disturbed) (Table 2). The shape of the *C. atlantica* dbh class distribution decreased in undisturbed stands and presented a unimodal mound-shaped form in logged and highly disturbed stands (Fig. 1; Supporting Information Table S1). Compared to undisturbed stands, the logged and highly disturbed stands showed a slightly higher tree density among intermediate-sized trees (30 cm < dbh $\leqslant$ 50 cm). In contrast, in undisturbed stands, both smaller (dbh $\leqslant$ 20 cm) and larger (dbh $\geqslant$ 50 cm) trees were more numerous. The difference was especially great in the smallest dbh class (dbh $\leqslant$ 10 cm). All stands exhibited diametric gaps in the higher dbh categories. The pooled dbh distribution in the highly disturbed stands differed significantly from that of the undisturbed and logged stands among lower size classes due to a large number of individuals in the 20–40 cm dbh size classes.

The mean diameter of *Q. ilex* trees ranged from 18.2 cm at the highly disturbed site to 2.5 cm at the logged site, with a high abundance of individuals in the smaller size classes being detected at the disturbed site (Fig. 1; Supporting Information Table S1). The shape of the dbh class distribution exhibited a unimodal mound-shaped form in the undisturbed and highly disturbed stands and was nearly exponential in the logged area, showing a descending mound-shaped function. Among the deciduous trees species *C. laciniata* and *A. monspessulanum,* unimodal dbh distributions dominated in the undisturbed and highly disturbed stands, whereas a bimodal distribution was observed in logged stands.

3.2. C. atlantica colonization and demography

The age data from all samples ($N = 310$) and the recruitment history at the study site suggested that the forests were even aged (two dominant age classes) (Fig. 2). The oldest tree in the stand

Table 2
Structural characteristics of the four main tree species among three management types in Ifrane National Park, Morocco. Values are means ± S.E. Different letters indicate significant post hoc differences between management types at $P \leqslant 0.05$ level based on Tukey's test. *Values significantly different; ns = non significant ($P < 0.05$; Students t-test).

Management type	Species	Adult density (ha⁻¹)	Diameter (cm)	Height (m)	Basal area (m² ha⁻¹)	Tall sapling density (ha⁻¹) (height ⩾ 130 cm and dbh < 5 cm)	Juvenile density (ha⁻¹) (5 ⩽ dbh < 10 cm)
Undisturbed	*Cedrus atlantica*	244.4 ± 40.1b	48.2 ± 12.9a	18.2 ± 2.1 ns	46.5 ± 12.7b	0	22.2 ± 14.7a
	Quercus ilex	161.1 ± 33.8a	13.1 ± 2.7a	5.8 ± 0.5b	1.82 ± 0.9a	27.8 ± 20 ns	155.6 ± 38.9a
	Cratagus laciniata	16.7 ± 9.6	7.5 ± 0.7	3.8 ± 0.5	0.06 ± 0.01	16.7 ± 3.7*	33.3 ± 16.7 ns
	Acer monspessulanum	11.1 ± 11.1 ns	6.9 ± 1.3*	4.8 ± 2.1 ns	0.04 ± 0.01*	5.6 ± 5.6	11.1 ± 5.6
Logged	*Cedrus atlantica*	283.3 ± 57.7b	49 ± 10.2a	21.8 ± 4.3 ns	56.5 ± 7.4ab	0	16.7 ± 9.6a
	Quercus ilex	5.6 ± 5.6c	2.5 ± 2.5b	1.1 ± 1.1c	0.01 ± 0.01b	0	22.2 ± 22.2 b
	Cratagus laciniata	0	0	0	0	5.6 ± 5.6	38.9 ± 14.7 ns
	Acer monspessulanum	16.7 ± 9.6 ns	18.9 ± 9.7	4.3 ± 2.4 ns	0.4 ± 0.05	0	0
Highly disturbed	*Cedrus atlantica*	622.2 ± 73.5a	36.6 ± 0.9a	20.2 ± 0.8 ns	66.6 ± 5.6a	0	27.8 ± 20.0a
	Quercus ilex	5.6 ± 5.6b	18.2 ± 5.6a	10.1 ± 3.8a	0.14 ± 0.1b	11.1 ± 11.1 ns	5.6 ± 5.6 b
	Cratagus laciniata	0	0	0	0	0	0
	Acer monspessulanum	0	0	0	0	0	0

was 401 years old, dating from 1610, but the majority of the aged trees entered the population during the 19th and 20th centuries (since 1800), only 14 of the cored trees were older than 200 years, and only 1 of these were older than 400 years. The population exhibited an establishment peak in the 1950s–1970s. In the highly disturbed stand, intensive tree establishment continued throughout this 20-year period. The logged and undisturbed sites exhibited fairly continuous recruitment between 1750 and 1900, with recruitment occurring more continuously after 1910.

3.3. Spatial patterns

Fig. 3 shows the spatial distribution of the main tree species in the study area based on x–y coordinates and describes the typical vertical structure for each type of forest. The high frequency and basal area proportion of *C. atlantica* indicate that the contemporary forest is dominated by this species, regardless of what kind of management it received. *Q. ilex* exhibits a moderate density (Table 2, Fig. 4) in undisturbed and logged forest, making it the main species in the natural understory of *C. atlantica* forests, together with *C. laciniata* and *A. monspessulanum*. In highly disturbed forests, the understory is composed of *C. atlantica* juveniles and *Q. ilex* at low densities, with *C. laciniata* and *A. monspessulanum* being almost absent.

The vertical structure (Fig. 3) gives us an idea of what kind of forest is promoted by human disturbance. While in the natural areas, it was observed that there were multiple tree species in an irregular canopy as well as wolf trees and a spatially diverse understory, in the logged and highly disturbed stands, a simpler structure was observed with an absence of very old trees dispersed in the forest, low regeneration, and a very low diversity of tree species. In disturbed areas, a higher density of *C. atlantica* was observed, which might be even higher than in undisturbed or logged stands; however, most of these trees showed small live crowns and live under high competition conditions.

Spatial analysis shows a general trend toward aggregation, independent of the species involved (Figs. 4 and 5). The relationships between trees were stronger in undisturbed areas and extend over greater distances (up to 9 m in undisturbed areas), but only up to 7 m in highly disturbed ones, and the clusters were usually larger in undisturbed sites (radius of 3–5 m in natural versus 1–2 m in logged areas). In logged forests, no clear relationship was observed because of the different responses of the different plots. The results

in this case were not significant for either L(r) and O-ring(r), and we can assume that there were no strong relationships. In undisturbed plots, univariate analysis revealed a strong tendency of *Q. ilex* toward aggregation in clusters with a radius of 1–3 m, as expected for a shade-tolerant species.

Intraspecific spatial analysis (Fig. 5) demonstrated that regeneration of *C. atlantica* and *Q. ilex* was facilitated by the presence of adult trees of these species. In the case of *Q. ilex*, the relationship was always positive but was only significant at distances of less than 5 m, producing clusters of regeneration around adult trees averaging 1–2 m. A similar pattern was observed for *C. atlantica*, where the relationship was significant for longer distances (>10 m) in 2 of 3 plots, creating clusters of regeneration of 2–4 m.

Analysis of the interspecific relationships between these two species (Fig. 5) revealed strong competition between *Q. ilex* and *C. atlantica* in undisturbed stands for distances of greater than 4 m. We can consider a 0 to 4 meter radius to represent a range in which there was an overlap of competition and short distance facilitation due to better soil surface humidity under the *C. atlantica* canopy.

4. Discussion

Studies on structure and dynamics in areas initially characterized by anthropic pressure can provide insight into the ecological mechanisms associated with silvicultural practices (Oliver and Larson, 1990; North et al., 2004). The present study performed along a management intensity gradient in *Cedrus atlantica* forests in the Middle Atlas (Morocco) shows that the dbh distribution and spatial agreement are powerful tools for understanding the structure and regeneration processes of a long-lived conifer species.

4.1. Size structure and species succesional pattern

In the investigated forest stands, *C. atlantica* and *Quercus ilex* are the major components of the forest in terms of both density and basal area. Deil (1982) and Derridj (1990) have studied the population structure of *C. atlantica* communities in similar ecological situations. They suggest that *C. atlantica* probably becomes established as a dense cohort following a severe disturbance (e.g., forest harvesting) and continues to regenerate in large tree-fall gaps. The current recruitment of *C. atlantica* in undisturbed and highly disturbed stands is apparently greater than in logged stands, although these differences were not significant.
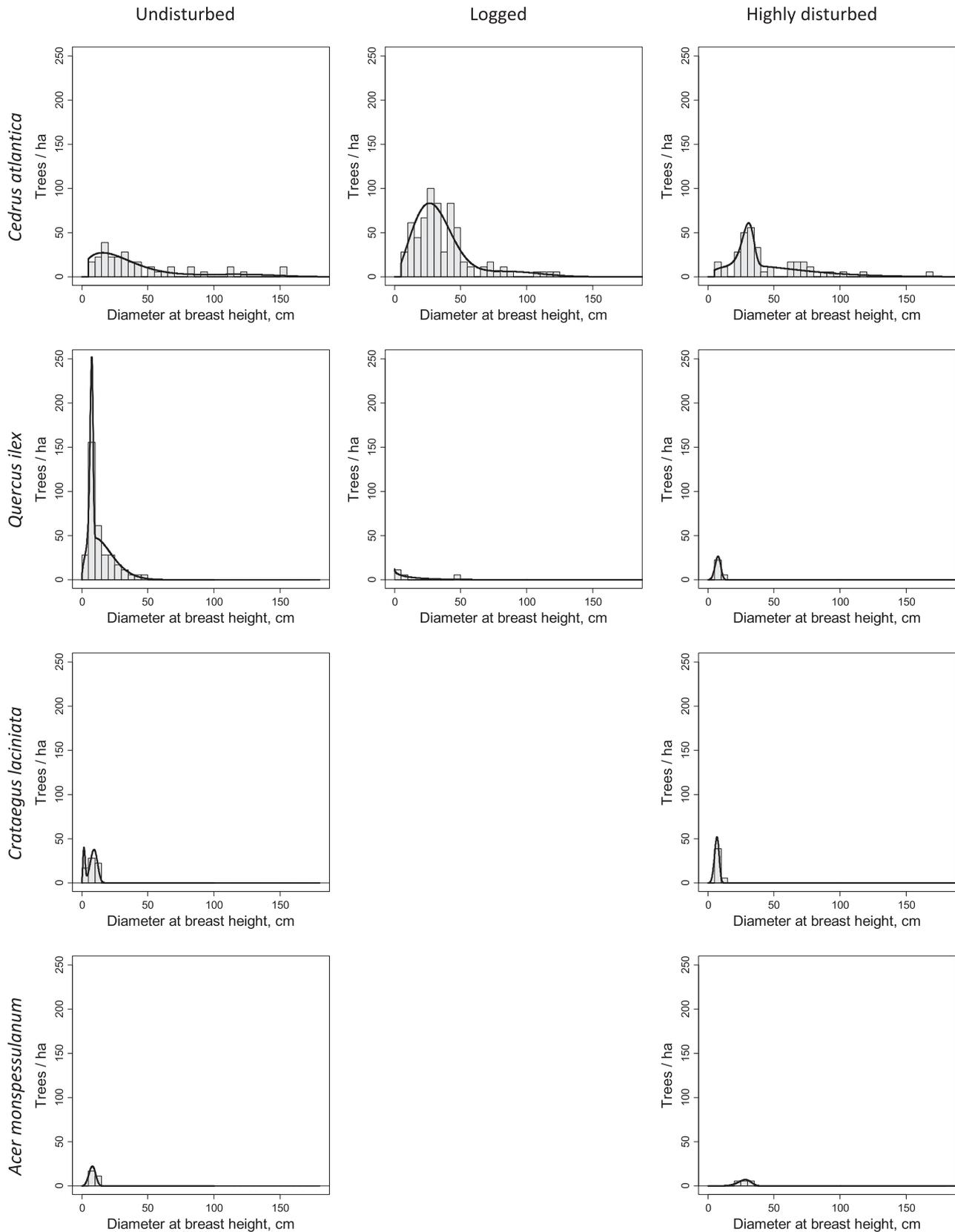
Fig. 1. Number of trees per hectare in 5-cm diameter classes, and their corresponding fitted diameter (dbh) distributions (solid line) for four tree species along a management gradient in Ifrane National Park, Morocco. Data were pooled from all study plots. The parameters of each diameter distribution per species and per management gradient are included in Supporting Information; Table S1.

Nevertheless, there is much debate over the level of perturbation necessary to maintain *Cedrus atlantica* populations and the mechanisms involved (Boydak, 2003; Et-tobi et al., 2009; Benzyane et al., 2009). This study showed that there are some limitations regarding the establishment of *C. atlantica* within the investigated forest environment under all three types of management. Seedlings are nonexistent, and the sapling and juvenile densities in these forests are lower than those suggested in the literature (Et-tobi et al., 2009). In general, all of the study areas presented low sapling and juvenile densities. The observed ratios of saplings to juvenile trees suggest that at present, *C. atlantica* is not regenerating successfully in forest sites of the Middle Atlas.

C. atlantica regeneration should be the result of replacement patterns, i.e., the balance between mortality and the different recruitment stages: seed production and viability, seed germination, seedling emergence, and seedling survival. The observed changes in the pattern of establishment indicate the potential of management practices to induce community shifts. The high densities of saplings and juveniles in highly disturbed stands may reflect the ability of *C. atlantica* to undergo rapid recruitment in disturbed forest areas due to seed inputs from old trees. The ability of *C. atlantica* to become established and grow in undisturbed and logged forests suggests that the failure of this species to regenerate below the canopy may depend on factors controlling its growth, such as soil resources, light levels, or temperature, rather than factors associated with fruit production, germination or seedling mortality (Krouchi et al., 2004). Because *C. atlantica* juveniles were much more numerous than tall saplings, regeneration appears to be a recent problem in these stands. As a consequence, the recruitment of juveniles may be occurring at a rate that is too low to maintain the existing adult population in these areas, and thus, a bottleneck in recruitment appears between the seedling (absent) and sapling stage, which has been shown for other *Cedrus spp.* forests (Boydak, 2003).

C. atlantica dynamics in the Atlas Mountains seems to be controlled by the interaction of processes operating on different scales. At local level, overgrazing, illegal cutting, and inadequate silvicultural practices destroyed a large proportion of seedling and sapling cohorts (Anonymous, 2007). At regional level, increasing drought and water stress related to climate change may cause a general decrease in the number of seedlings, and it is explained by the water requirements of germination, particularly in seasonally dry Mediterranean-type ecosystems (Lloret et al., 2009; Linares et al., 2011). Such trends in size distributions have previously been demonstrated for *C. atlantica* forests (Et-tobi et al., 2009) and are associated with population changes during stand development, including high mortality or suppression of seedlings and saplings. Moreover, the logged sites were harvested in the last 20 years (Anonymous, 2007), which could have led to changes in the age structure and regeneration of *C. atlantica* in the managed populations. The under representation of *C. atlantica* juveniles in the logged sites could be interpreted as a consequence of the low abundance of seedlings and saplings following the silvicultural treatments. In managed forests seedling recruitment and adult logged often occur on different time scales, and regeneration emerges over the course of longer periods, due to the density regulation, seed dispersal and seedling establishment (Deil, 1982; Ezzahiri and Belghazi, 2000). The difference between the change in relative seedling and adult abundance among the management levels suggests that climatic directional change may play an important role in the disconnection between recruitment and adult performance (Lloret et al., 2009; Linares et al., 2011), and produces rapid reactions in *C. atlantica* community's pattern of recruitment (Touchan et al., 2008; Et-tobi et al., 2009).

Q. ilex showed a better regeneration status in undisturbed forest. In the logged stands, this result could possibly be attributed to the effect of silviculture. Thinning modifies the dbh distribution by releasing suppressed trees, but maintaining a high tree density, such that understory tree regeneration layers (*Quercus ilex* in the present study) can be limited. This was observed due to the inclusion of small-sized trees. In contrast, in highly disturbed stands, the lack of *Q. ilex* regeneration may be attributed to overgrazing. *C. laciniata* and *Acer monspessulanum* regeneration was only observed in undisturbed and logged stands, showing the sensitivity of this species to human disturbance.

Using left-truncated and/or bimodal Weibull functions always resulted in better maximum likelihood estimates when fitting
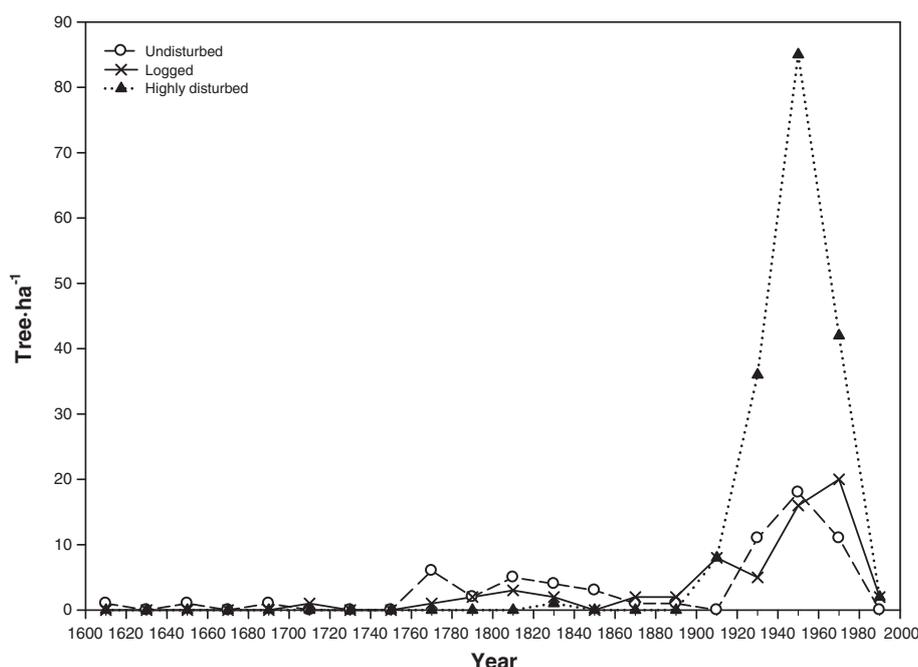
Fig. 2. Number of C. *atlantica* individuals established and still surviving over the past 400 years among three management types in Ifrane National Park, Morocco.
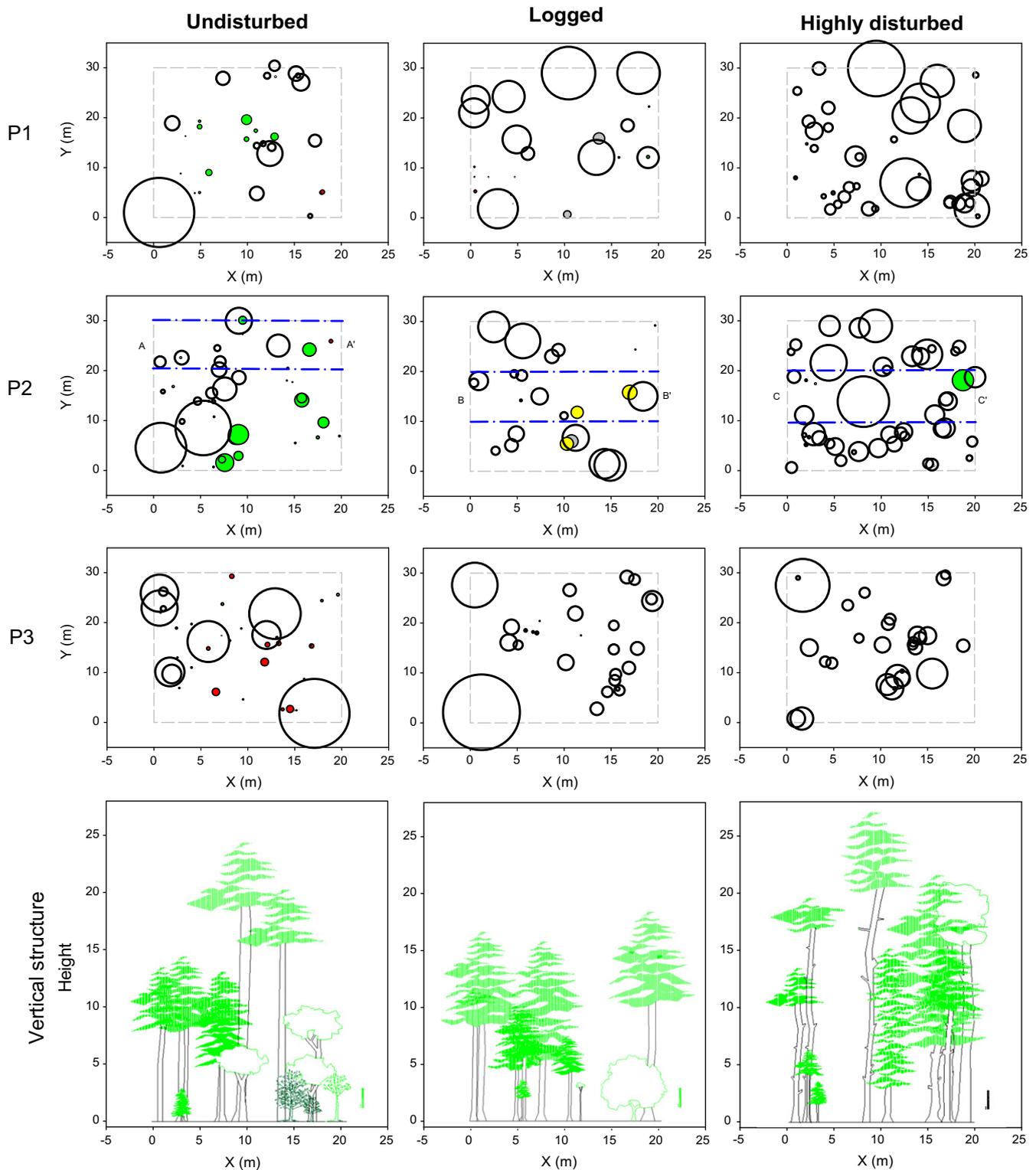
Fig. 3. Overhead projection map of tree crowns within three of the four study plots of each management type (P1, P2, P3). The outer boundary (solid line), which represents 30 × 40 m, is included to show crowns extending outside of the plot. The inner square (dashed line) indicates the 20 × 30-m dimensions of each plot. Species are indicated as follows: *C. atlantica*, white; *Q. ilex*, green; *C. laciniata*, yellow; and *A. monspessulanum*, red. The lower three graphs show the composite vertical structure of the three selected plots at each level of management.

diameter distributions of *C. atlantica*. For those species with very low frequency in a given site, the bimodal distribution based on finite mixtures either showed convergence problems or directly yielded the same results as the unimodal two-parameter Weibull distribution function. In the *C. atlantica*-dominated forests, the

shape of the dbh distributions differed significantly between the undisturbed, logged and highly disturbed stands (Fig. 1). Compared to undisturbed stands, the logged and highly disturbed stands exhibited a slightly higher tree density among intermediate-sized trees (30 cm < dbh ⩽ 50 cm). In contrast, in undisturbed stands,
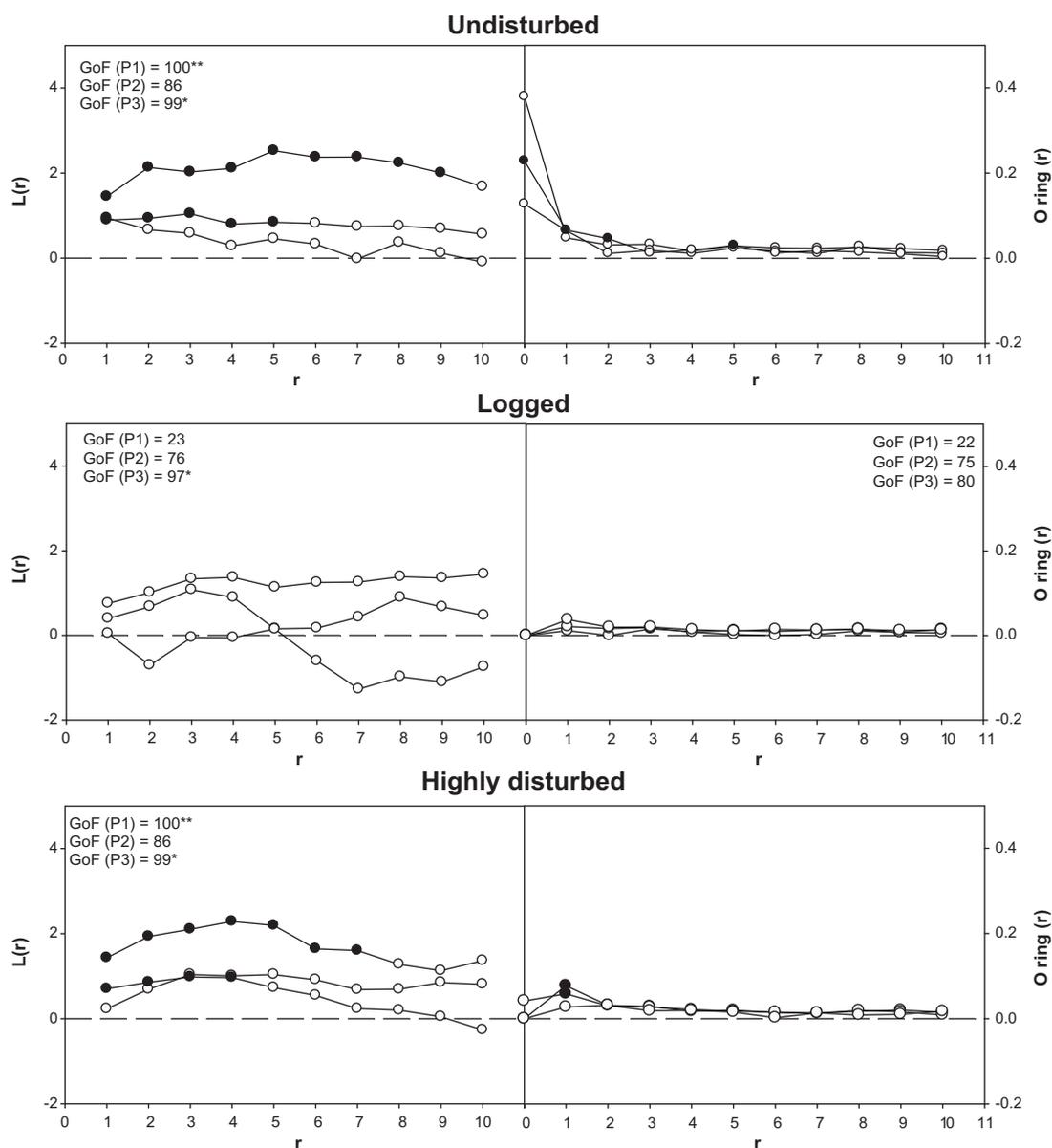
Fig. 4. Univariate spatial associations studied using second order functions (Ripley's L (left) and O-ring (right)) of *C. atlantica* trees in three levels of management. Solid circles represent significant relationships at distance r (α = 0.05) and open circles represent no significance. Goodness of fit (GOF) for each plot is also showed and *p*-value of each GOF is symbolized as * (*p* < 0.05) or ** (*p* < 0.001).

both smaller (dbh ⩽ 20 cm) and larger (dbh ⩾ 50 cm) trees were more numerous. This indicates that the stand structure was more complex in undisturbed stands. An obvious explanation for the lack of large trees in the logged stands is that they were logged selectively in the past. This was indeed the main method of logging until the 1950s. More recently, silvicultural thinnings from below have favored trees in the mid-diameter classes, while smaller understory trees have not been favored. As a consequence, a greater range of tree sizes were a typical feature of the dbh distributions in natural stands compared to manage ones (Crow and Perera, 2004). Again, the effect of thinnings can be observed on the dbh distribution due to the release of suppressed trees so that the understory tree layers can develop and through homogenizing the dbh distribution of *Cedrus* species. Additionally, the control of illegal logging in undisturbed stands may increase the number of young trees as result of natural regeneration starting from seeds provided by the remaining old trees, after setting-up of rigorous protection.

The dbh distributions observed for *Q. ilex* showed that there was usually a very short "tail" of large trees at low densities in the investigated stands. The shape of the dbh class distribution presented a unimodal mound-shaped form (Fig. 1) in undisturbed and higly disturbed stands and was nearly exponential in logged areas, showing a descending mound-shaped function, indicating an incipient regeneration process. In undisturbed stands, the overall tree density was higher compared to that of the logged and highly disturbed stands. This difference was mainly because the undisturbed stands exhibited a large number of trees in small and middle dbh classes. In natural stands, this often resulted in a descending dbh distribution, in which small trees were most abundant, and the density of trees declined with tree size.

A possible successional pattern detected was the greater number of small *Q. ilex* trees (saplings) in the undisturbed stands compared to the logged and highly disturbed stands. Continuous regeneration of *Q. ilex*, which is a shade-tolerant species, is typical
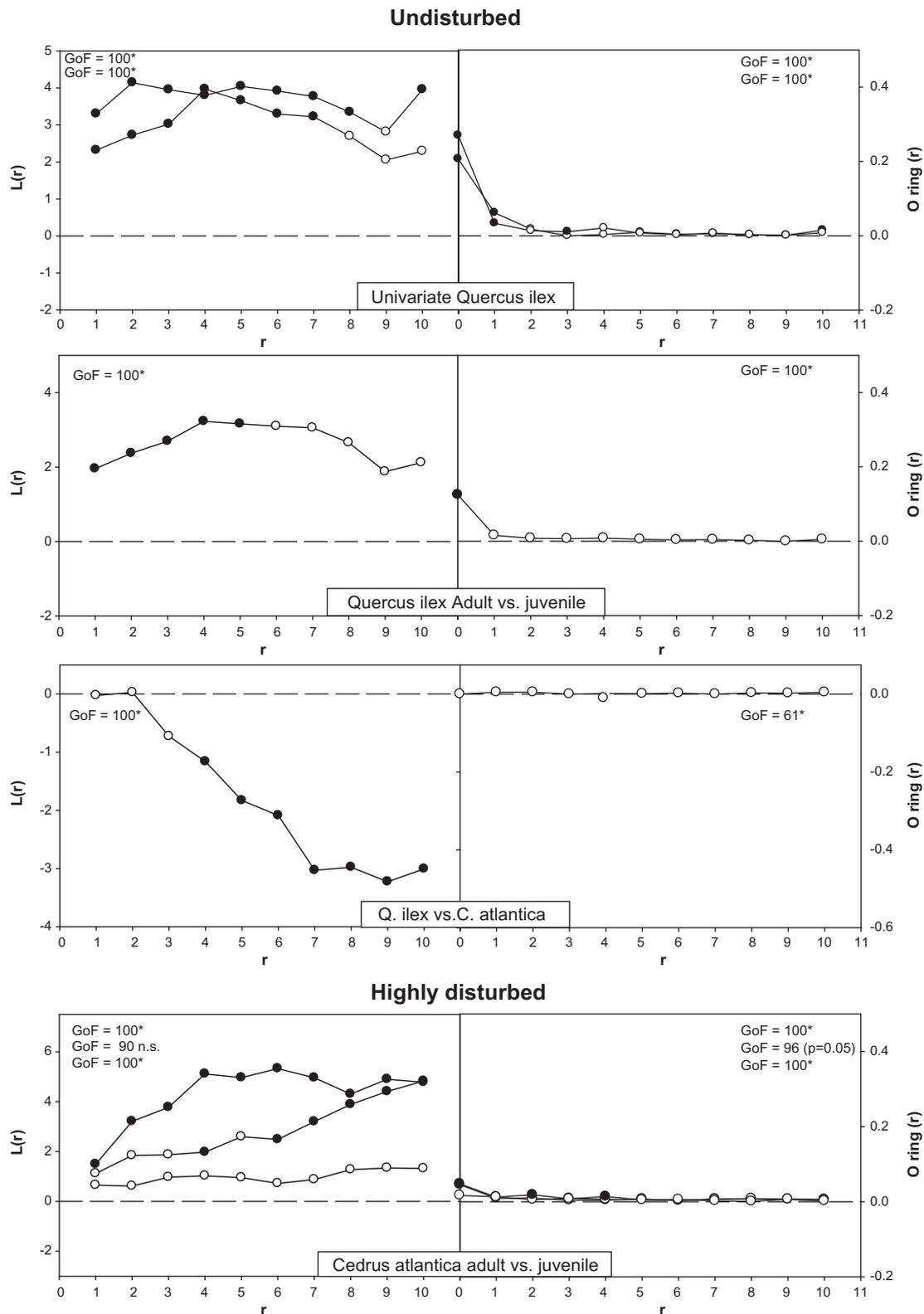
Fig. 5. Spatial associations in Undisturbed and Anthropized stands. Univariate relationships among *Q. ilex* trees, as well as bivariate relationships between adults and juveniles of *Q. ilex*, and between *Q. ilex* and *C. atlantica* trees, that are calculated using bivariate version of the same second order functions (L(r) and O-ring(r)). In anthropized stands only relationships between adults and juveniles trees was conducted due to the limited number of *Q. ilex*.

in dense forest areas in the absence of disturbance (Barbero et al., 1990; Benabid, 2000; Ajbilou et al., 2006). In the Middle Atlas, mature, open-canopy forests show evidence of continuous recruitment of *C. atlantica* and *Q. ilex*, suggesting a successional gradient ranging from sites dominated by *Cedrus* to those dominated by *Quercus* and mixed angiosperm species in response to forest disturbances. These results agree with the regeneration strategies of *C. atlantica* (Ezzahiri and Belghazi, 2000; Krouchi et al., 2004) as well

as the dynamic models proposed for coniferous mountain forests (van Pelt and Franklin, 2000) and the suggestion that different tree life histories produce distinct population size distributions. By 2011, the *Cedrus* forest had developed into a *C. atlantica*—*Q. ilex* forest, with high *Q. ilex* abundances in a well-structured managed forest characterized by a higher basal area and stem density of both species. Without perturbations, *Q. ilex*, which is more shade-tolerant, is becoming established and increasing in terms of its basal area in the studied locations, particularly in undisturbed areas. Similar characteristics have been observed in other mixed *Cedrus-Quercus* forests (Benabid, 2000; Ezzahiri and Belghazi, 2000), supporting the hypothesis of a negative relationship between the symmetry of the population size distributions of *C. atlantica* and *Q. ilex* trees. Old-growth mixed *C. atlantica-Q. ilex* forests are characterized by an equilibrium between *C. atlantica* and *Q. ilex* (Ezzahiri and Belghazi, 2000), suggesting that stands in which there are large *C. atlantica* individuals and an abundant presence of *Q. ilex* (undisturbed) are better conserved. The majority of the young population became established during the 20th century (since 1910). In the anthropized site, intensive tree establishment was particularly high in the 1950s.

4.2. Spatial patterns

We suggest that a more complete understanding of the impact of management practices can be gained by considering both the spatial and temporal patterns of tree establishment (Fortin and Dale, 2005). *C. atlantica* stem maps and univariate analysis indicate a broad dispersion of stems. Spatial analyses indicate that both *C. atlantica* and *Q. ilex* have positive relationships among all their age-classes, while the interespecific relationship show some facilitation (in all probability due to the ability of *Q. ilex* to grow under canopy at short stages) at very short distances but a general strong negative effects possibly due to competition for water resources.

C. atlantica showed pronounced spatial aggregation in undisturbed stands at different scales. This aggregation may result largely from the interaction between adult and young *Cedrus* trees as also suggests the bivariate analysis (Fig. 5). In natural *Cedrus-Quercus* forests, smaller openings between older *Cedrus* trees are colonized directly by *Q. ilex*. In these areas, *Q. ilex* likely benefited from non-intervention and the small openings associated with *Cedrus* gaps close to seed sources and within the zones of influence of neighboring trees (Gómez-Aparicio et al., 2008). The clumping of *C. atlantica* could reflect the proximity to parent trees (driven by seed dispersal), together with the fact that young to adult *C. atlantica* require full sun to regenerate (Toth, 1978). Regeneration within these openings was ensured by the broad dispersion of parent trees, and young individuals were situated within 20–30 m of the nearest seed source, well within the range of abundant seed rain (Toth, 1978; Ezzahiri and Belghazi, 2000). Alternatively, this aggregation could reflect the heterogeneity of the site conditions, with regeneration of *C. atlantica* being limited to the same types of microsites. However, this seems improbable given the auto-ecological character of this species (Quézel, 1983; Ezzahiri and Belghazi, 2000) and the uniformity of the topography, soils, and vegetation in the study area. In *C. atlantica-Q. ilex* forests, facilitation of *Q. ilex* under *C. atlantica* openings in older stands has important consequences for the rate and pattern of vegetation change, initially by accelerating the pace at which *Q. ilex* forests may replace *C. atlantica* and subsequently by slowing the structural (subcanopy) development of older forests. As a result, the spatial and temporal dynamics of undisturbed forests can vary according to the management practices applied (e.g., Motta and Nola, 2001; Lingua et al., 2008).

On highly disturbed stands, *C. atlantica* also showed spatial aggregation but at shorter distances than in the undisturbed ones,

and general structure may suggest a different origin for that relationship. Under these conditions, small openings in *C. atlantica* related to grazing were primarily colonized by *Cedrus* from seed sources widely distributed throughout the remnant stands. Although *Q. ilex* trees were present in the understory, they occurred at a considerably lower density and had no interaction with *C. atlantica*. In contrast, *C. atlantica* did not show clear spatial aggregation patterns at any distance in the logged forests.

Inferring biotic interactions from spatial patterns clearly requires caution. Positive associations could be explained by facilitation but also by similar patterns of dispersal or responses to the environment (Baumeister and Callaway, 2006). Likewise, negative associations could indicate inhibition or competition but also contrasting responses to a heterogeneous environment or indirect effects mediated by another species. Species life histories, the relative timing of establishment, the environmental context, and the spatial scale are important considerations in distinguishing among these alternatives (Zenner, 2000; Fortin and Dale, 2005). Several explanations are possible for the pronounced aggregation of young conspecific stems over a broad range of spatial scales. Thus, although *Q. ilex* was numerically less important than *C. atlantica*, its ability to become established under cedar canopy and form new foci for recruitment appears to be important in the dynamic process as might be inferred by the absence of competition between the two species in short distances (<3 m). Facilitation by conspecific stems of *Q. ilex* is also likely to have contributed to rapid infilling of undisturbed and managed sites. Facilitation can occur through moderation of microclimatic stress, suppression of competing vegetation, or the cumulative effects of trees on soil properties (Baumeister and Callaway, 2006). The positive association between young and old *C. atlantica* suggests that such facilitation effects may persist, shaping the longer-term development of these forests. Similar shifts over time in the balance of positive and negative effects have been observed between nurse and protected plants in other Mediterranean and coniferous forests (Debussche and Lepart, 1992; van Pelt and Franklin, 2000; Kennedy and Sousa, 2006; Lingua et al., 2008).

4.3. Implications for management and suggestions for further research

Comparison of the structures and dynamics of *C. atlantica* patterns in the Arzou and Sidi ́MGuid forests illustrates that the level of management applied may produce significant changes in the structure and dynamics of population sizes and dynamic regeneration processes. The present study also shows that *C. atlantica* is able to thrive under an extremely high degree of human pressure, although the lack of seedlings and small saplings indicate perturbation of the regeneration of *C. atlantica* along a gradient of management levels. To investigate the possible mechanisms associated with this situation, it would be interesting to study additional *C. atlantica* sites associated with different management levels and livestock (ungulate) densities. In the Arzou and Sidi ́MGuid forests, development of the forests in the absence of intervention has been studied by means of enclosure patches in which seed sources or large saplings of other species are already present (undisturbed sites), giving rise to new research questions. For example, are native tree and shrub species able to compete with *C. atlantica* in the absence of herbivory, and will *C. atlantica* continue to undergo recruitment in the understory of *C. atlantica-Q. ilex* forests? Particular attention should be dedicated to patches in which both *C. atlantica* and other native shrub species, such as *C. lacianta* and *Acer monspessulanum*, are present because of the ecology of these species (Benabid, 2000). Thus, a decrease in silvicultural and anthropic pressure could lead to a change in the further development of the forest. The structure and dynamics of *C. atlantica-Q. ilex* forests are expected to have been greatly tempered over time and space

by human activities in Morocco. These populations require more attention for conservation and protection efforts.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.10.011.

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