



Characterizing spatial structure of *Abies marocana* forest through point pattern analysis

Mariem Ben-Said (Ben-Said, M.)^{1*}, Abdelilah Ghallab (Ghallab, A.)², Hajar Lamrhari (Lamrhari, H.)³, José Antonio Carreira (Carreira, J.A.)⁴, Juan Carlos Linares (Linares, J.C.)⁵, Lahcen Taïqui (Taïqui, L.)¹

¹Applied Biology and Pathology Laboratory, Department of Biology, Faculty of Sciences, 93002, Abdelmalek Essaâdi University, Tetouan, Morocco.

²Service des Etudes d'Aménagement et de Planification, 93000, Direction Régionale des Eaux et Forêts et de la Lutte Contre la Désertification du Rif, Tétouan, Maroc.

³Applied Botany Laboratory, Department of Biology, Faculty of Sciences, 93002, Abdelmalek Essaâdi University, Tetouan, Morocco.

⁴Departamento de Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, 23071 Jaén, Spain. ⁵Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, 41013 Sevilla, Spain.

Abstract

Aim of study: Understanding small-scale patterns caused by stochastic factors or community interactions driving forest structure and diversity of Moroccan fir *Abies marocana* Trab.

Area of study: Talassemtane fir forest, Talassemtane National Park, Rif Mountains, northern Morocco.

Material and methods: Eight plots representative of the structural variability of *A. marocana* forests were selected, and all tree individuals with diameter at breast height (dbh) ≥ 2 cm were mapped and measured. We performed four types of spatial point pattern analyses: (1) Univariate analyses to explore the overall trees spatial pattern, (2) bivariate analyses to assess the spatial relationship between juveniles and *A. marocana* adults, (3) correlation between tree sizes (dbh) and distance between points pairs using the univariate mark correlation function, and (4) random labeling analysis between dominant and suppressed Moroccan fir individuals to assess competition patterns.

Main results: We found a strong spatial aggregation of fir individuals and a positive intraspecific association between juveniles and adult trees. However, there were weak but significant distance-dependent effect on tree size and density-dependent effect on suppression pattern.

Research highlights: Shade-tolerance, seed dispersal and/or microsite heterogeneity might play important roles in the observed fir patterns. Our results provide a basic knowledge on within-stand Moroccan fir spatial distribution, with implications for adaptive management of these relic forests, and prompting to further research to test advanced hypotheses.

Keywords: Moroccan fir; Talassemtane National Park; Rif forest; Spatial analysis; summary statistics; facilitation; aggregation.

Abbreviations used: MF (Moroccan fir); Talassemtane National Park (TNP); dbh (diameter at breast height); Univariate pair-correlation function ($g(r)$); Heterogeneous Poisson (HP); Bivariate pair-correlation function ($g_{12}(r)$); Univariate mark correlation function ($k_{mm}(r)$), Mark connection function ($p_{12}(r)$).

Authors' contributions: Conceived the idea, designed the study and wrote the manuscript: MB and LT. All authors designed the methodology. Conducted fieldwork: MB, LT, JAC and JCL. Performed the analyses and interpreted the results: MB with contribution of LT. All authors contributed critically to the drafts and gave final approval for publication.

Citation: Ben-Said, M., Ghallab, A., Lamrhari, H., Carreira, J.A., Linares, J.C., Taïqui, L. (2020). Characterizing spatial structure of *Abies marocana* forest through point pattern analysis. *Forest Systems*, Volume 29, Issue 2, e014. <https://doi.org/10.5424/fs/2020292-16754>.

Supplementary material: Figures S1 to S5 accompany the paper on FS's website.

Received: 27 Mar 2020 **Accepted:** 25 Aug 2020

Copyright © 2020 INIA. This is an open access article distributed under the terms of the Creative Commons Attribution 4.0 International (CC-by 4.0) License.

Funding: The authors received no specific funding for this work.

Competing interests: The authors have declared that no competing interests exist.

Correspondence should be addressed to Mariem Ben-Said: mariembensaid20@gmail.com

Introduction

Understanding patterns and scales driving stand structure and diversity is a main topic of forest ecology (Legendre & Legendre, 1998). Forest dynamics drives the trees' spatial patterns, while this spatial structure also determines to a large degree the properties of the whole forest ecosystem (Gadow *et al.*, 2012). Specific processes generate particular patterns of growth and regeneration

leading to upcontrasting structural arrangements (Gadow *et al.*, 2012). Spatial pattern influences key aspects of ecosystem functions, including disturbance resistance and recovery dynamics, regeneration, snow retention, and habitat quality, as has been studied in fire-prone pine and mixed-conifer forests (Churchill *et al.*, 2013). Hence, spatially explicit approaches are widely recommended for ecosystem management (Gadow *et al.*, 2012). In the case of endangered tree species, spatial pattern analyses might

be useful to guide conservation purposes (Raventós *et al.*, 2011).

Consequently, stand structure and diversity has received increasing interest from forest managers in the recent decade (Schall *et al.*, 2018). Multiple stand structural attributes characterize stand types, affecting management and driving the stand productivity (Schall *et al.*, 2018). Fine-scale spatial structure is generally assessed by point pattern analyses based on second-order statistics of the overall point-to-point distances in a mapped region (Legendre & Legendre, 1998). These statistics provide a key tool for identifying spatial pattern types and scales and allow concluding if a pattern is clumped, regular or random (Legendre & Legendre, 1998; Wiegand & Moloney, 2004). Processes controlling spatial patterns of forest species has been investigated by point pattern analyses in temperate (Getzin *et al.*, 2006, Carrer *et al.*, 2018), tropical (Wiegand *et al.*, 2007) and Mediterranean regions (Raventós *et al.*, 2010, García-Cervigón *et al.*, 2017). Here we focused on the Moroccan fir, *Abies marocana* Trab., a North African Tertiary relict species of the group of circum-mediterranean firs (Linares, 2011). This species has sometimes been considered as a subspecies of the Spanish fir, *Abies pinsapo* Boiss. Other authors suggested to split it into two species, *Abies marocana* and *A. tazao-tana* Côzar ex Hug. Villar (Arista & Talavera, 1994; Farjon, 2010). More recent molecular and biometric studies have converged towards the separation of the Moroccan and Spanish firs (Sękiewicz *et al.*, 2013, Dering *et al.*, 2014). In the present study we adopted the classification of Fennane *et al.*, (1999) considering Moroccan fir within a single endemic species.

Despite MF is included in a protected area, increasing human pressure, particularly by forest clearance for the expansion of *Cannabis* cultivation, logging, pollarding and grazing is still present. Furthermore, it is a drought-sensitive species, considered highly vulnerable to expected global warming during the second half of the 21st century (Sánchez-Salguero *et al.*, 2017). Three decades ago, Melhaoui (1990) reported a lack of natural regeneration of MF and suggested two main causes: summer water stress and overgrazing by goats. Recently, Linares *et al.*, (2011) reported a high regeneration dynamic of this species. Castello *et al.*, (2016) found that MF population was structurally sustainable, whereas the combined fir populations in Spain and Morocco were structurally unsustainable due to excessive mortality. Actually, the species dynamic is not well understood while there is an urgent need to develop studies that inform conservation management.

The aim of this study was to assess spatial patterns of the Moroccan fir in forest stands in order to explore underlying processes. Given limited seed dispersal by wind in this fir and its tolerance to shade, we hypothesized intraspecific spatial aggregation patterns. These patterns of aggregation were tested by applying a univariate analysis

and considering the location of stems (analysis 1). Spatial distribution of juveniles, relative to adult trees, was explored by a bivariate spatial analysis (analysis 2). Continuous size data (dbh) was included in marked point pattern analysis (analysis 3) to test the effect of proximity assuming that the dbh of two neighboring points tend to be smaller if they exhibit a competitive interaction (negative correlation), while they tend to have larger dbh than expected when a facilitative interaction is operating (positive correlation) (Getzin *et al.*, 2006, 2008; Illian *et al.*, 2008; Wiegand & Moloney, 2014). In the case of denser stands intraspecific competition may be strong and result in tree suppression or even mortality. We evaluated density-dependent suppression by random labeling analysis (analysis 4) of the relative distribution of dominant vs suppressed trees (Gavríkov & Stoyan, 1995). If suppressed trees are close to dominant ones we expect a one-sided intraspecific competition, whereas a symmetric competition would be inferred in the case of aggregation of suppressed individuals and their segregation from dominant trees (Raventós *et al.*, 2010; Wiegand & Moloney, 2014).

Materials and Methods

Species and study site

Moroccan fir (MF) is located in a quaternary refuge with exceptional high moisture conditions, in the core area of Talassemrane National Park (TNP) in Northern Morocco. The area is included, since 2006, in the Mediterranean Intercontinental Biosphere Reserve of Spain and Morocco, established by the UNESCO's Man and the Biosphere Program. Its forests have been recognized as a biodiversity hotspots and a centre of endemism (Médail & Diadema, 2009). Moroccan fir is on the IUCN Red List as a globally threatened species in the category "Endangered" (Alaoui *et al.*, 2011).

The study was carried out in the main distribution area of *A. marocana* at the TNP located in the western Rif Mountains, Chefchaoun, Morocco (Fig. 1). MF is distributed within two main forests: the Jbel Tazaout, accounting for about 300 ha and the Talassemrane range, accounting for about 3760 ha. MF is restricted to limestone and dolomitic substrates, at elevations between 1500 and 2000 m, on north, east and west slopes, in Mediterranean humid and perhumid bioclimates. In the upper limit of its area, MF is progressively replaced by the Atlas cedar *Cedrus atlantica* (Endl.) Carrière, while the Maghreb maritime pine *Pinus pinaster* Aiton subsp. *hamiltonii* var. *maghrebiana* Hugué del Villar dominates the lower part with the holm oak *Quercus ilex* L. and black pine *Pinus nigra* Arnold subsp. *mauretanica* (Maire and Peyer.) Heywood (Aafi, 2000). Soils are predominantly Alfisols and Mollisols developed on calcareous and dolomitic

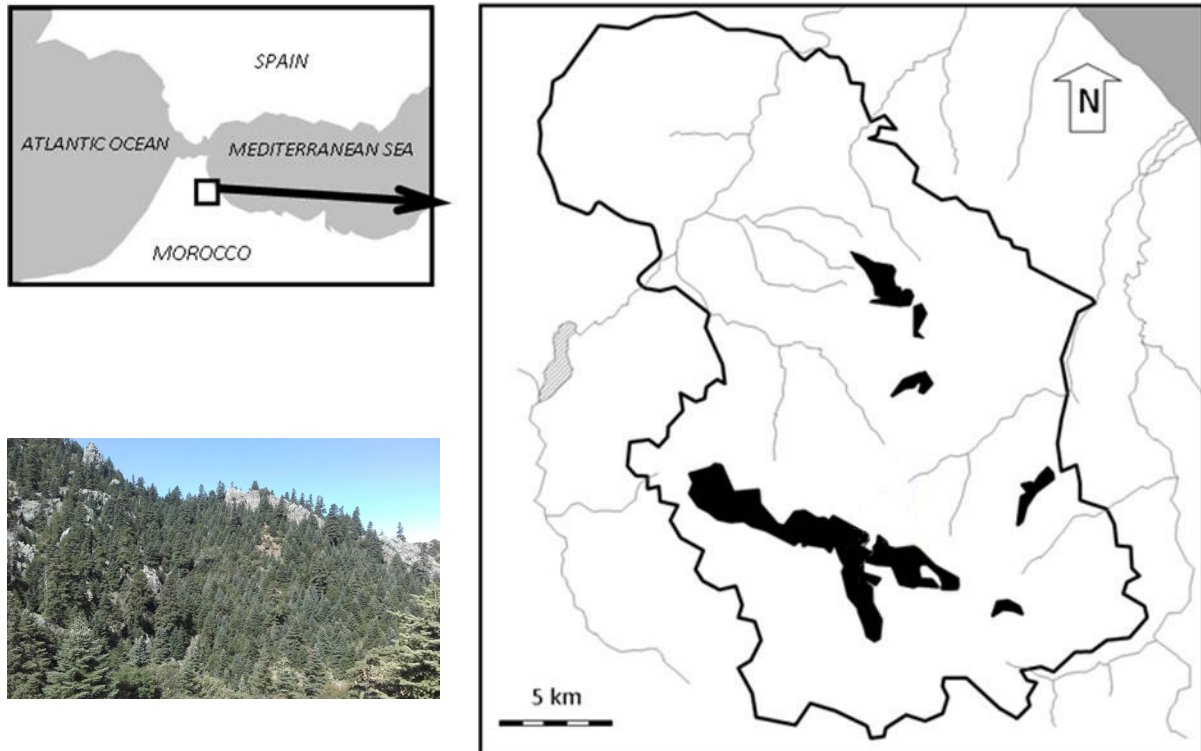


Figure 1. Location of the study area within the Talassemtane National Park. Shaded area shows the main *Abies marocana* forests.

parent material (Benjelloun, 1993). Annual rainfall varies between 500 mm in the eastern valleys and more than 1500 mm on the high mountain peaks (Jbel Lakrâa 2156 m). The snow is present but occasional (Benabid, 2000). Mean temperature is around of 12-14 °C and extreme values for the mean of absolute maxima and absolute minima are 33°C and -3°C, respectively (Ghallab & Taïqui, 2015).

Field sampling

We sampled eight plots located in MF stands at the TNP with radius of 15 to 20 m depending on topography, for instance rock outcrops. In each plot, we recorded the distance of all trees to the center of plots and their azimuth, in order to determine their coordinates (x, y). A total of 908 trees (including 670 MF) were registered and measured, with a mean of 113 trees per plot. For each tree, we measured the diameter at breast height (dbh) of all individuals with $dbh \geq 2$ cm. The status of trees was labeled as dominant individuals, suppressed individuals (trees green canopy only in the upper third), snags (standing dead trees), logs (downed dead wood) and stumps (cut-surface). We recorded the coordinates and topographic characteristics of each plot (elevation, aspect, and slope) in the field by means of a global positioning system (GPS). Observed signs of disturbance or human impacts were registered (fire, cutting, grazing, trampling). The

field work was carried out during the spring of 2010 and the summer of 2017.

Data analysis

Stand characterization

Density of stems (trees ha^{-1}) with $dbh \geq 2$ cm was calculated for MF in each of the eight plots as well as its basal area ($m^2 ha^{-1}$), mean dbh (cm) and the percentage of adults ($dbh > 10$ cm) and juveniles ($2 \leq dbh \leq 10$ cm). For other conifers and broad-leaved species, only stem densities are reported in this article. The analysis of these structural elements allows making an overall description of sampled plots. For each plot, the distribution of dbh was assembled on 5-cm classes. $H' = - \sum_{i=1}^S pi \ln(pi)$, was calculated both for woody species (pi corresponding to the proportion of trees being to the i -th species and S the number of woody species), and for dbh (pi representing the fraction of individuals belonging to the i -th dbh class and S the number of size classes) (Buongiorno *et al.*, 1994).

Spatial pattern analyses

Analysis 1: We used the univariate pair-correlation function $g(r)$ to measure both the intensity and scale the

tree spatial pattern (Ripley, 1977; Stoyan & Stoyan, 1994; Wiegand & Moloney, 2004; Law *et al.*, 2009). The $g(r)$ is the expected number of points of the pattern at distance r from an arbitrary point of the pattern, divided by the pattern intensity λ in the plot (Wiegand & Moloney, 2004). It is calculated in the same way as Ripley's K-function but with replacement of circles by rings, which gives to $g(r)$ a non-cumulative character (Stoyan & Stoyan, 1994). In univariate analyses the Complete Spatial Randomness (CSR) is by far the most used null model (Velázquez *et al.*, 2016) under which: $g(r) = 1$, $g(r) > 1$ for aggregation while $g(r) < 1$ for segregation. Because of the heterogeneity present in the plots, a Heterogeneous Poisson (HP) null model was used which assumes that the pattern intensity λ varies slightly with location (x, y) (Stoyan & Stoyan, 1994; Wiegand & Moloney, 2014). HP takes into account forest heterogeneity and thus reflects realistically tree-to-tree interactions (Carrer *et al.*, 2018).

Analysis 2: We used a bivariate version of the pair-correlation function $g_{12}(r)$ to assess the relationship between adults ($\text{dbh} > 10 \text{ cm}$) and MF juveniles ($2 \leq \text{dbh} \leq 10 \text{ cm}$). It analyzes the association between all pairs of points of two patterns. The $g_{12}(r)$ is the density of pattern 2 points (juveniles in our case) at distance r from a typical point of pattern 1 (adults) divided by the density λ_2 of pattern 2 points (Raventós *et al.*, 2011). For this analysis, we tested the antecedent condition hypothesis (Wiegand & Moloney, 2004) by randomizing the position of the juveniles (pattern 2) and keeping the position of the adults (pattern 1) fixed. This null model is largely used in young-adult associations (Carrer *et al.* 2013, Velázquez *et al.* 2016) since it is applied for situations when two types of points are not created at the same time, but in sequence (Szymt, 2014), which is the case of juvenile-adult relationships. Under antecedent condition, there is independence, attraction or repulsion for $g_{12}(r) = 1$, $g_{12}(r) > 1$ or $g_{12}(r) < 1$, respectively.

Analysis 3: In addition to point pattern locations, other information can be integrated in the analysis, usually called as "marks" such as tree size (dbh in our case) (Wiegand & Moloney, 2004). Effect of intraspecific interaction on individual growth was analyzed using univariate mark correlation function $k_{mm}(r)$ which quantifies the similitude or dissimilitude between the marks m_i and m_j of two neighboring fir trees i and j , separated by distance r (Illian *et al.*, 2008; Wiegand & Moloney, 2014). It corresponds to the test function of size product $f(m_i, m_j) = m_i * m_j$ normalized by division by the squared mean mark for all marks in the plot (Getzin *et al.*, 2008). If $k_{mm}(r) > 1$, the two trees tend to have larger dbh than average marks when they are nearby (*e.g.* positive correlation), while a value of $k_{mm}(r) < 1$ indicates individuals tend to have smaller dbh (*e.g.* negative correlation), and if $k_{mm}(r) = 1$ the two marks are independently assigned

to individuals (Illian *et al.*, 2008; Wiegand & Moloney, 2014). We used the independent marking null model that randomly shuffles the mark among all MF individuals (Wiegand & Moloney, 2014). It assumes that dbh values are independent of individual location (Stoyan & Stoyan, 1994).

Analysis 4: We used random labeling null-model to test partial-pair correlation function and mark connection function of two categories of MF trees: suppressed trees *vs* trees in good condition (hereafter referred to as dominant trees). As suggested by Goreaud & Pélissier (2003), random labeling null model is appropriate when such categories are considered to result mainly from different growing conditions affecting *a posteriori* a single population. The bivariate pair correlation has been defined in analysis 2 and it is applied here to test attraction *vs* repulsion among these two patterns (suppressed and dominant trees) under random labeling null model. The mark connection function $p_{12}(r)$ describes the probability of suppression of MF trees in dependence of the distance r to conspecific trees (Gavrikov & Stoyan, 1995; Illian *et al.*, 2008). Under random labeling, $p_{12}(r) = p_1 p_2$, where p_2 is the proportion of suppressed trees among all MF individual. For $p_{12}(r) < p_1 p_2$, suppressed trees and trees dominant trees are segregated at distance r within all individuals while larger values of p_{12} indicate a positive association (Gavrikov & Stoyan, 1995; Raventós *et al.*, 2010).

For each type of analysis, data from the eight sampled plots were combined inside one average function (Illian *et al.*, 2008; Wiegand & Moloney, 2014) to serve as statistical replicates. The eight sampled plots have been selected according to conditions of replicate analysis (same study area, within a limited range of environmental variation) from a total of 19 original plots. The common method is to estimate the statistical functions separately for each plot and then to aggregate the estimates in one mean overall test statistic (Illian *et al.* 2008). Practically, we performed data analysis for each plot separately, and then we combined the results into a single summary statistic and produce the associated simulation envelopes. *Programita*® (<https://programita.org>), a software for spatial point pattern analysis in Ecology, uses an aggregation formula in which the estimator of the O-ring statistic is combined with that of the intensity (Equations 3.107 and 3.108 in Wiegand & Moloney, 2014, p. 249-250) to obtain the final aggregated estimator of each test function.

For all analyses and for each null model we performed 199 Monte Carlo simulations of the envelope limits between fifth lowest and highest values (Wiegand & Moloney, 2014). If the curve of observed function fall outside the upper simulation envelope there is a positive association (aggregation or attraction), while if the empirical curve is below the lower simulation envelope a negative association is expected (segregation or repulsion). Finally,

the patterns are independent if the observed function is fitting inside simulation envelopes. To assess the ability of the null models to reflect the data we used a goodness-of-fit test GoF (Loosmore & Ford, 2006).

All spatial pattern analyses were done with *Programita* software (Wiegand & Moloney, 2014).

Results

Stand composition and characteristics

Moroccan fir density, basal area and tree size and other structural characteristics across the eight studied plots are

given in Table 1. MF Maximum density and highest basal area were recorded in plot 3 with 1386 trees ha⁻¹ and 68.9 m² ha⁻¹, respectively; the minimum ones in plot 7 and plot 6 with 392.6 trees ha⁻¹ and 19.1 m² ha⁻¹, respectively. The percentage of juveniles was higher than that of adults in plots situated at higher altitudes. Mean dbh of MF was the highest in the low elevation plot 2 (20.6 cm) and smaller in plots 3 to 6 (similar mean values around 13 cm) (Table 1).

In terms of MF status, the densest plot (plot 3) contained the highest density of suppressed and dead trees (580.0 and 155.6 trees ha⁻¹, respectively, Table 1). Conversely, less dense plots generally showed lower density values of dead wood which did not exceed 8.0 trees ha⁻¹

Table 1. Main geographic, topographic and structural characteristics of sampled plots in Moroccan fir forest

Plots		1	2	3	4	5	6	7	8
Latitude (N)		35°14027	35°151110	35°137780	35°143170	35°137778	35°111389	35°121389	35°116667
Longitude (W)		-5°14090	-5°141194	-5°140350	-5°140210	-5°121389	-5°133889	-5°068056	-5°056389
Elevation (m a.s.l)		1743	1620	1760	1694	1715	1420	1550	1450
Aspect		NE	SE	NE	NW	NNW	W	NE	NW
Slope (°)		22	24	7	45	20	5	35	35
<i>Abies marocana</i> (trees ha ⁻¹)	Total Density	628.7 (75)	891.2 (63)	1386.3 (98)	1075.1 (76)	676.4 (85)	557.0 (70)	392.6 (111)	732.1 (92)
	Juveniles	397.9 (47)	396.1 (28)	961.9 (68)	622.4 (44)	429.7 (54)	286.5 (36)	208.7 (59)	445.6 (56)
	Adults	230.8 (28)	503.6 (35)	424.4 (30)	452.7 (32)	246.7 (31)	270.6 (34)	183.9 (52)	286.5 (36)
	Dominant	302.4 (37)	608.3 (43)	622.5 (44)	693.2 (49)	103.5 (13)	87.5 (11)	113.2 (32)	95.5 (12)
	Suppressed	302.4 (35)	155.7 (11)	580 (41)	268.8 (19)	421.8 (53)	413.8 (52)	198.1 (56)	509.3 (64)
	Dead	8	70.8	155.6	99	87.5	0.0	14.1	31.8
	Stump	16	56.6	28.3	14.2	63.7	55.7	67.2	95.5
<i>Cedrus atlantica</i> (trees ha ⁻¹)		206.9	141.5	396.1	84.9	254.6	23.9	0	0
<i>Pinus nigra</i> (trees ha ⁻¹)		63.7	0	0	56.6	0	0	0	0
<i>Juniperus oxycedrus</i> (trees ha ⁻¹)		15.9	0	0	424.4	0	31.8	0	0
<i>Acer granatense</i> (trees ha ⁻¹)		0	171.1	14.1	14.1	15.9	23.9	28.3	55.7
<i>Crataegus laciniata</i> (trees ha ⁻¹)		8	0	14.1	56.6	0	0	0	0
<i>Quercus ilex</i> (trees ha ⁻¹)		0	0	0	0	0	302.4	0	23.9
<i>Quercus faginea</i> (trees ha ⁻¹)		0	0	0	0	0	15.9	0	0
<i>Taxus baccata</i> (trees ha ⁻¹)		0	0	0	0	39.8	23.9	0	0
<i>Ilex aquifolium</i> (trees ha ⁻¹)		0	0	0	0	0	8.0	0	0
<i>Viburnum tinus</i> (trees ha ⁻¹)		0	0	0	0	0	0	0	23.9
<i>Abies marocana</i> basal area (m ² ha ⁻¹)		27.4	60.8	68.9	34	22.2	19.1	58.9	49.8
<i>Abies marocana</i> mean dbh ± SD (cm)		14.7 ± 18.5	20.6 ± 21.2	13.6 ± 21.2	13.8 ± 14.6	13.0 ± 15.8	13.7 ± 15.2	18.5 ± 22.6	17.8 ± 23.5
H' species		0.89	0.76	0.61	1.05	0.80	1.09	0.25	0.50
H' dbh		1.9	2.19	1.72	1.87	1.73	1.69	1.82	1.68

In the present study, we considered as juveniles individuals with $2 \leq \text{dbh} \leq 10$ cm and as adults those with $\text{dbh} > 10$ cm. For Moroccan fir, we estimated tree status as: dead individuals (snags and logs), suppressed and stumps. For the other species, only the total density is shown. Number of Moroccan fir individuals included in spatial analyses is shown between brackets for each plot

in plot 1 and was absent in plot 6. Plot 8 contained the highest density of stumps (95.5 stem ha⁻¹) followed by plots 7 and 5 (67.2 and 63.7 trees ha⁻¹, respectively, Table 1).

There were other woody species that were classified into two groups (Table 1): conifers (mainly *Cedrus atlantica*, *Juniperus oxycedrus* and *Pinus. mauretanica*) and broad-leaved species (mainly *Acer granatense* and *Crataegus laciniata*). *Cedrus atlantica* was the second dominant species (after MF). Its density reached 396.1 trees ha⁻¹ in plot 3. Despite its low density, *Acer granatense* was found in all except one plot. Other important species occurred to a lesser extent, such as *Pinus nigra*, *Juniperus oxycedrus* and *Crataegus laciniata*. The plot 6 comprised almost all these species and thus presented the highest Shannon's species diversity index (H' species, Table 1), while plots 7 and 8 had the lower values of H' species (with 0.25 and 0.5, respectively). The highest value of H' (dbh) was found in plot 2 (H'dbh=2.19), whereas the smallest values were recorded in plots 8 and 6 (1.68 and 1.69, respectively).

Diameter distribution of MF in all sampled plots showed reverse-J shape (Fig. 2) with a high number of trees in the smaller size classes but wider size classes were relatively rare. All plots showed diameter distribution peak in the smallest dbh class (2–5 cm), and all had stems until the diameter range of 30–35 cm. Plots 1, 2 and 3 presented the larger diameter distribution, while plot 4 did not contain individuals larger than 55 cm of dbh.

Spatial pattern of Moroccan fir

The number of Moroccan fir individuals included in spatial pattern analyses is reported between brackets for each plot in Table 1 and the locations of all measured trees by plot are reported in Figure S1 [suppl.]. Result of univariate pair correlation function using all MF trees is shown in Figure 3a. The $g(r)$ of the replicated plots indicated a

significant aggregation ($p = 0.005$) up to 3 m. Individuals of MF have more conspecifics in their close neighborhood than expected by the null model. Bivariate analysis of the relationship between MF juveniles ($2 \leq \text{dbh} \leq 10$ cm) and adults ($\text{dbh} > 10$ cm) showed a strong significant attraction between the two size classes in the combined plots up to 2 m ($p = 0.005$, Fig. 3b). Juveniles were clearly more aggregated around adult trees than expected by the null model.

The mark-correlation functions $k_{mm}(r)$ showed a non-significant negative correlation ($p = 0.015$) up to a distance of 2 m and at 9–11 m. This indicated that sizes of MF individuals were independently distributed from their location (Fig. 4a). Finally, for the random labeling analysis, the pair correlation function $g_{12}(r)$ showed a weak but significant departure from the null model at 2.5–3.5 m ($p = 0.005$, Fig. 4b). This indicates that there is repulsion between suppressed and dominant individuals. The mark connection function $p_{12}(r)$ revealed similar results; a negative association between dominant and suppressed trees is shown at a small-scale of 2.5–3.5 m ($p = 0.005$, Fig. 4c). Consequently, when randomly selecting two points with this scale r there was a high probability that both were dominant or that both were suppressed.

Discussion

The density of young trees was higher than that of adults in all except one plot and reached 961.9 trees ha⁻¹ in plot 3 (Table 1). The frequency distribution of tree dbh classes showed an overall J-reverse shape reflecting a good regeneration capacity with a prompt decline in the abundance of larger-size trees (Fig. 2). Similar results were found by Linares *et al.*, (2011) and recently by Navarro-Cerrillo *et al.* (2020) in TNP. Tree density and basal area were higher at high elevation and were associated with increasing rates of mortality. Besides, the percentage

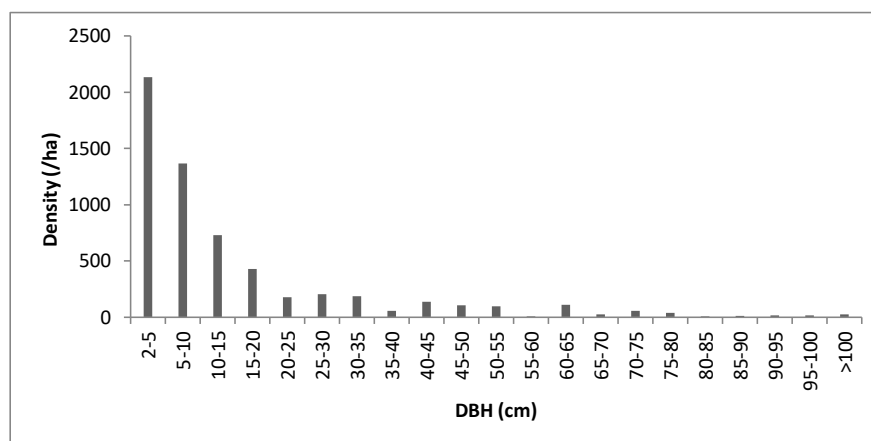


Figure 2. Frequency distribution of diameter at breast height (dbh) of *Abies marocana* in all sampled plots.

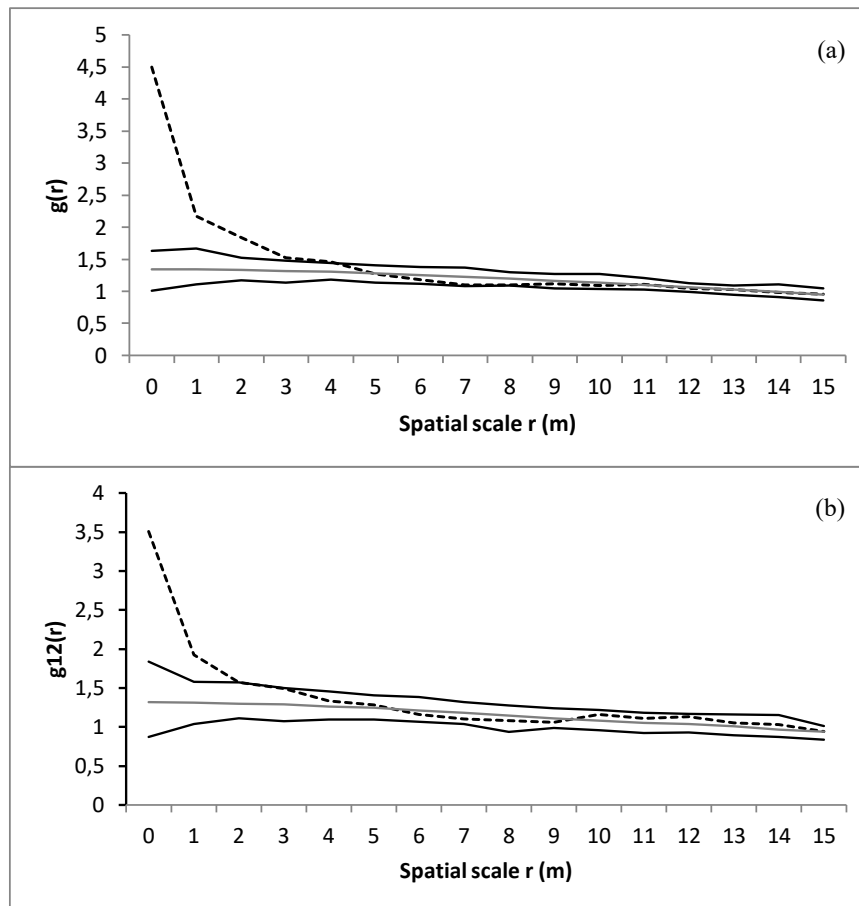


Figure 3. (a) Univariate pair correlation function $g(r)$ of the overall *Abies marocana*. (b) Bivariate pair correlation function $g_{12}(r)$ of two fir size classes: juveniles with dbh ≤ 10 cm (pattern 2) and adult trees with dbh > 10 cm (pattern 1). Dotted line indicates the empirical curve, gray line indicates the expected value under the null model (Heterogeneous Poisson for univariate $g(r)$ and independence for bivariate $g_{12}(r)$) and black lines indicate limits of 199 Monte Carlo simulation envelopes.

of young trees increased as elevation did, while mean tree diameter was relatively higher at lower elevation (Table 1). A similar decrease of tree height as elevation rises has been reported by Benabid (1982). The resulting diversity of tree sizes is lower at low altitude. Regarding species richness, overall diversity of woody species was relatively higher at middle and lower elevations (plots 4 and 6).

MF attained relatively higher mean dbh values in less dense stands (plots 2 and 7) which have lower values of Shannon's dbh index (H' dbh, Table 1). Similar relationships between size diversity, wood species diversity and stand density were found by Linares *et al.*, (2011). Compared to Spanish fir forests, MF forests are characterized by higher species diversity (Aafi, 2000; Benabid, 2000; Linares *et al.*, 2011) due to the presence of several tree species mainly *C. atlantica*, *A. granatense*, *P. nigra* and *J. oxycedrus*. The presence of these species with their structural features described in the present study was similar to the results found by Navarro-Cerrillo *et al.* (2020).

Nevertheless, our results also support other environmental factors affecting MF forest structure and diversity.

Hence, stumps frequency, especially of small sized trees indicating human perturbation, mainly at low elevation (plots 8, 7, 6, 5 and 2). In the Rif, forests have deeply suffered from an abusive exploitation since the protectorate period (Benabid, 2002) which was reflected by the absence of very large size classes (Fig. 2). However, before this period, the exploitation by local populations was relatively less important although it has considerably increased over last decades (Benabid, 2002). In a comparison between Moroccan and Spanish fir stands, Linares *et al.*, (2011) reported a widespread logging activity by local inhabitants in Talassemtane forest. Furthermore, anthropogenic pressure, especially the extension of *Cannabis* crops, remains a major threat to the maintenance of MF forests (Benabid, 2000; Taïqui, 2005). Previous studies reported the predominance of these crops at low altitudes; however, at present, *Cannabis* crops are increasingly becoming the main driver of deforestation of MF and other mountainous forests in Northern Morocco.

We found a significant spatial aggregation of Moroccan fir trees, at a fine scale of up to 3 m, as showed by the

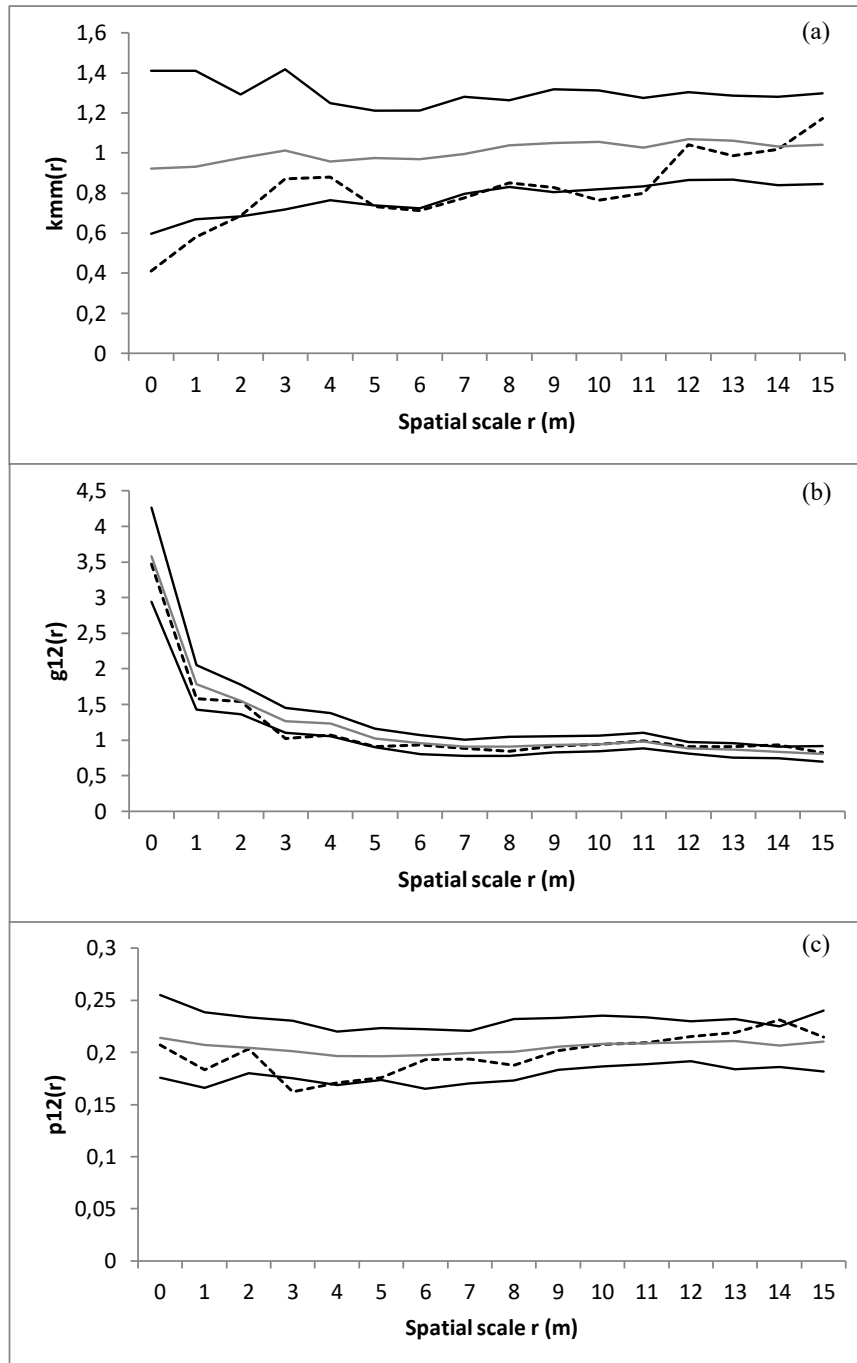


Figure 4. (a) Univariate mark-correlation function $k_{mm}(r)$ of *Abies marocana* tree size (dbh). (b) Random labeling analysis of firs (living trees vs suppressed trees) using partial-pair correlation functions $g_{12}(r)$ and (c) mark connection function $p_{12}(r)$. Dotted line indicates the empirical curve, gray line indicates the expected value under the null model (independent marking for $k_{mm}(r)$ and random labeling for $g_{12}(r)$ and $p_{12}(r)$) and black lines indicate limits of 199 Monte Carlo simulation envelopes.

univariate pair-correlation function (Fig. 3a). This result is refined by the bivariate analysis of two size classes; MF young individuals are mainly concentrated around adult trees at small-scale (up to 2 m; Fig. 3b). Additionally, marked point pattern analyses showed that individual tree dbh is independently distributed from location, which indicate that aggregation does not affect tree size (Fig. 4a). As su-

ggested for other Mediterranean ecosystems (De Luis *et al.*, 2008), the observed MF pattern may be produced by a combination of various mechanisms including its limited seed dispersal, shade tolerance and the ecological effects of spatial heterogeneity of resources and conditions. The general context of climatic stress and human pressure should be also considered.

Spatial patterns of tree species usually show a scale-dependent aggregation that is generated by seed dispersal limitation (De Luis *et al.*, 2008; Zhang *et al.*, 2013). Wind dispersal can cause short distance dissemination away from source leading to seed shadow around adult trees (Wiegand *et al.*, 2007). Seeds that did not dispersed far from adult trees are accumulated under the crowns so that few juveniles are found far from the adult stems (LeMay *et al.*, 2009; Raventós *et al.*, 2011; García-Cervigón *et al.*, 2017). Like other Mediterranean firs and pines (García-Cervigón *et al.*, 2017; Abellanas & Pérez Moreno, 2018), MF seeds are wind-dispersed. Melhaoui (1990) estimated that the dispersal distance of MF is almost always less than 5 m. Our finding supports this estimation since the aggregation of juveniles around MF adults occurred up to 2 m (Fig. 3b).

However, seedling establishment at short distance from adults depends on species preferences and it is usually thought to be affected by spatial heterogeneity and its effects on habitat quality (Zhang *et al.*, 2013). For example, shade tolerance or intolerance abilities can play an important role in species spatial pattern (Abellanas & Pérez-Moreno, 2018). But unlike wet sites where seedlings development is strongly influenced by light (Chave, 2000), the limiting factor at dry sites seems to be moisture where large trees offer moister microsites to small trees (LeMay *et al.*, 2009). In our case, like the majority of fir species, MF is a shade-tolerant species that regenerate under canopy layer (Baumer, 1977). Previous studies on MF also found that the moisture factor plays a crucial role in natural regeneration (Melhaoui, 1990). Clumping of MF juveniles under adult trees is due to the favorable moisture conditions below canopy and shade-tolerance ability of juveniles.

Taking separately, almost all plots showed aggregated pattern of MF trees. The exceptions were plots 6 and 8 for the univariate analysis and plots 5 and 8 for the bivariate one, which showed random and independent patterns, respectively (Fig. S2 and S3 [suppl.]). These departures from the general findings might be explained by a higher anthropogenic pressure reflected by the high amount of stumps in these plots. Indeed, many studies reported that anthropogenic activities such as logging can modify the spatial structure of the stand (Motta & Edouard, 2005).

In addition to seed dispersal limitation and environmental heterogeneity, biotic interactions play an important role in the dynamics of an ecosystem and can induce specific structures (Goreaud & Péliissier, 2003). Previous studies have used second order statistics to study the relationships between spatial patterns and biotic processes, and have reported positive, independent and negative correlations between tree positions and sizes. In a study of *Pistacia atlantica* in a semi-arid region of Iran (Erfanifard *et al.*, 2018), bivariate analysis revealed a spatial ag-

gregation of saplings around females while mark analysis using $k_{mm}(r)$ showed a negative correlation between dbh and position. In this case, aggregation negatively affects size. In a large study area covering 30 ha in a temperate old-growth forest in China, Zhang *et al.*, (2013) identified mostly independence of tree dbh at greater distances using $k_{mm}(r)$, but highly significant negative correlation at short distances for the majority of species and some cases of significant short-distance attraction of dbh associated with the light-demanding shrub species. Jácome-Flores *et al.*, (2016) found at Martinazo site in Spain a clustered distribution of dwarf palms *Chamaerops humilis* individuals while their size did not show a spatial correlation. They suggested that this result can be seen when using small sample sizes, which produce noticeably wider simulation envelopes. Getzin *et al.*, (2008) showed no correlation of the studied marks (dbh, crown area and upper crown area) using $k_{mm}(r)$ at all scales in a low-density deciduous stand in Germany which imply low overall competition effect. Similar results were found for *Pinus sylvestris* in Poland where no correlation was found between trees either using diameter or height of pine individuals (Erfanifard & Stereńczak, 2017). Law *et al.*, (2009) reported that the absence of correlation may suggest that the size is much more equally distributed over space than the individuals are themselves. In our study, mark correlation analysis of *Abies marocana* trees in Talassemtane forest showed a non-significant negative correlation of tree sizes up to 2 m, as well as at 9-11 m where a negligible negative correlation appeared (Fig. 4a). This non-significant negative correlation may be attributed to the occurrence of a weak competitive effect at small distance. Negative correlation indicates aggregation of young individuals and may be related to clumped dispersal and establishment patterns, which are absent at later developmental stages due to competition and mortality.

At the plot level, we found no correlation of tree sizes except for plot 2 which showed a very weak and non-significant negative correlation up to a very short distance (< 0.5 m) (Fig. S4 [suppl.]). The significant pattern detected by the average function at small scale based on replicated pattern could be reinforced by the additional effect of weak negative correlation tendency observed in plots 5, 7 and 8 (where the $k_{mm}(r)$ expected value was closed to the lower simulation envelope). However, the facilitative effect recorded among young and aged trees may hide the competitive effect occurring within groups of regenerating individuals.

Furthermore, low density of suppressed trees as well as their spatial pattern confirms weak competitive interaction and self-thinning process. In fact, the result of random labeling either by $g_{12}(r)$ or $p_{12}(r)$ showed a weak but significant repulsion between suppressed and dominant individuals at 2.5-3.5 m ($p = 0.005$, Fig. 4b and 4c). The highest density of suppressed trees in association with a higher

rate of dead trees in the densest plot 3 (Table 1) may indicate a density-dependent suppression process but which could be significantly detected by test functions only at a limited scale. This negative association appears to be a small-scale pattern only emerging within a 2.5–3.5 m range which reflects a fine patchy pattern where small and almost distinct groups of dominant and suppressed trees occur separately within the stands (Carrer *et al.*, 2013). As most of the suppressed trees were small trees, and MF regeneration was abundant in most plots, the spatial negative correlation in tree size could contribute sporadically to suppression of tree growing close to each other in denser stands. Accordingly, MF juveniles clumped in the shelter of the adults and benefit from a positive recruitment interaction which seems to be more important than an intra-specific competitive effect.

Here, the random labeling considered for each plot showed the distinct behavior of the four last plots (Fig. S5 [suppl.]), and thus support the previous observations in the three other analysis types (Fig. S2, S3 and S4 [suppl.]). Indeed, a negative association between dominant and suppressed trees is found in plots 5, 8 and particularly 7 which extends to 4.5 m, in addition to a significant positive association at distance of > 14 m shown in this last plot. At the small scale, suppressed trees appear to be separated from dominant ones while they are more grouped at larger scale.

Under current climate conditions and human pressure in TNP (Taïqui, 2005; Linares *et al.*, 2011; Ghallab & Taïqui, 2015), seedlings and saplings of Moroccan fir regenerate and maintain themselves in favorable moisture conditions under the canopy of adult trees thanks to their shade tolerance and the absence of significant intraspecific competitive effect. Spatial intraspecific negative interaction may sometimes be undetectable because MF can withstand competition for light since it is a shade tolerant species (Baumer, 1977; Abellanas & Pérez-Moreno, 2018). This suggests that intraspecific competition did not appear to be a major process that negatively affects MF growth in the studied stands, which is just the opposite of what was found for the Spanish fir counterpart (Linares *et al.*, 2010). In contrast, the facilitative interaction where parents provide shelter from abiotic stress and protection against biotic consumption was more relevant.

Although our study has provided insights into the spatial patterns of Moroccan fir, there are some limitations regarding the relative number of points used within each plot, particularly in the case of analyses involving two pattern types. Indeed, Wiegand & Moloney (2014) recommended the use of 50–70 individuals as a minimum in spatial point analyses. However, Velázquez *et al.* (2016) reported that many studies used relatively few individuals in point pattern analysis (< 100). For instance, Camarero *et al.* (2000) used at least 15 indi-

viduals, Zenner & Peck (2009) used 20 individuals. More recently, Janík *et al.* (2016) and Cordero *et al.* (2016) used much less trees (10 and 4, respectively). In our case, we had a sufficient number of trees in univariate analyses, and despite that the available number of trees was split into two classes in the bivariate and random labeling analyses, this limitation was minimized by using replicate analysis with data from the eight sampled plots that were combined into one average function (Illian *et al.*, 2008; Wiegand & Moloney, 2014). This method is a straight-forward extension of the typical analysis of separate plots (De Luis *et al.*, 2008) and allows increasing the sample size and the statistical power (Illian *et al.*, 2008). Although being considered as an extension of the common analysis of isolated plots (De Luis *et al.*, 2008), replicate analysis was rarely used by ecologists in spatial point patterns (but see Raventós *et al.*, 2011).

The results of our explanatory study allowed us to describe the overall spatial pattern of the Moroccan endemic fir. Analysis of the main MF structural characteristics in the sampled plots indicated a remarkable regeneration dynamic. However, the anthropic pressure remains a serious problem which constitutes a constraint to MF community preservation. Moroccan fir showed strong positive intraspecific association and juveniles were significantly attracted to adult trees. We highlight the importance of shade tolerance, seed dispersal and microsite heterogeneity in the observed facilitative intraspecific effect. However, more investigation is needed to test subsequent hypothesis, in particular by integrating other species (*e.g.* *Cedrus atlantica*). Understanding spatial structure and dynamics of trees, especially endemic species, is critical particularly in the context of global change.

Acknowledgements

The authors thank Ouazzani Hamza, Benjamín Viñepla, Lucia Alvarez and Jamal Eddine Salhi for their help in the field. We thank also the staff of the “National Park of Talassemtane” and of “La direction provinciale des eaux et forêts et de la lutte contre la désertification de Chefchaouen” for their logistic support. Ben-Said Mariem thanks Fadoua Asraoui and Farida Berrad for their different helps during the study period.

References

- Aafi A, 2000. Floristic diversity of Morocco's fir ecosystem (*Abies maroccana* Trab.) (Talassemtane National Park). *Nature et Faune* 18 (1): 15–19.
- Abellanas B, Pérez-Moreno PJ, 2018. Assessing spatial dynamics of a *Pinus nigra* subsp. *salzmannii* natural

- stand combining point and polygon patterns analysis. For *Ecol Manage* 424: 136-153. <https://doi.org/10.1016/j.foreco.2018.04.050>
- Alaoui ML, Knees S, Gardner M, 2011. *Abies pinsapo* var. *marocana*, Moroccan Fir. The IUCN Red List of Threatened Species 2011: E.T34126A9841418. URL: <http://www.iucnredlist.org/details/34126/0>
- Arista M, Talavera S, 1994. Phenology and anatomy of the reproductive phase of *Abies pinsapo* Boiss. (*Pinaceae*). *B J Linn Soc* 116: 223-234. <https://doi.org/10.1111/j.1095-8339.1994.tb00431.x>
- Baumer M, 1977. Le sapin du Maroc. R.F .F ., XXIX: 343-354. <https://doi.org/10.4267/2042/21153>
- Benabid A, 1982. Etude phytoécologique, biogéographique et dynamique des associations sylvatiques du Rif occidental. Problèmes posés par la réforestation et l'aménagement des peuplements forestiers actuels. Doctoral thesis, Université St Jérôme-Marseille.
- Benabid A, 2000. Flore et écosystèmes du Maroc: Évaluation et préservation. Ibis Press, Paris, France. 359 pp.
- Benabid A, 2002. Le Rif et le Moyen-Atlas (Maroc): Biodiversité, Menaces, Préservation. Mountains High Summit Conference for Africa. UNEP, Kenya (Nairobi) May 6-10.
- Benjelloun H, 1993. Soil genesis, classification, and nitrogen cycling in forest ecosystems of the Northwestern Rif region of Morocco. Doctoral thesis, Oregon State University, USA.
- Buongiorno J., Dahir S., Lu H.C., and Lin C.R., 1994. Tree size diversity and economic returns in uneven-aged forest stands. *For Sci* 40: 83-103.
- Camarero JJ, Gutiérrez E, Fortin MJ, 2000. Spatial pattern of subalpine forest-alpine grassland ecotones in the Spanish Central Pyrenees. *For Ecol Manage* 134: 1-16. [https://doi.org/10.1016/S0378-1127\(99\)00241-8](https://doi.org/10.1016/S0378-1127(99)00241-8)
- Carrer M, Soraruf L, Lingua E, 2013. Convergent space - time tree regeneration patterns along an elevation gradient at high altitude in the Alps. *For Ecol Manage* 304: 1-9. <https://doi.org/10.1016/j.foreco.2013.04.025>
- Carrer M, Castagneri D, Popa I, Pividori M, Lingua E, 2018. Tree spatial patterns and stand attributes in temperate forests: The importance of plot size, sampling design, and null model. *For Ecol Manage* 407: 125-134. <https://doi.org/10.1016/j.foreco.2017.10.041>
- Castello J D, Cale JA, Angelo CMD, Linares JC, 2016. Baseline Mortality Analysis Reveals Legacy of Contrasting Land Use Practices on the Structural Sustainability of Endangered Moroccan and Spanish Mountain Forests. *Forests* 7: 1-12. <https://doi.org/10.3390/f7080172>
- Chave J, 2000. Dynamique spatio-temporelle de la forêt tropicale. *Ann Phys Fr* 25: 1-184. <https://doi.org/10.1051/anphys:200006001>
- Churchill DJ, Larson AJ, Dahlgreen MC, Franklin JF, Hessburg PF, Lutz JA, 2013. Restoring forest resilience: From reference spatial patterns to silvicultural prescriptions and monitoring. *For Ecol Manage* 291: 442-457. <https://doi.org/10.1016/j.foreco.2012.11.007>
- Cordero I, Jiménez MD, Delgado JA, Villegas L, Balaguer L, 2016. Spatial and demographic structure of tara stands (*Caesalpinia spinosa*) in Peru: Influence of present and past forest management. *For Ecol Manage* 377: 71-82. <https://doi.org/10.1016/j.foreco.2016.06.034>
- Dering M, Sękiewicz K, Boratyńska K, Litkowiec M, Iszkuło G, Romo A, Boratyńska A, 2014. Genetic diversity and inter-specific relations of western Mediterranean relic *Abies* taxa as compared to the Iberian *A. alba*. *Flora* 209: 367-374. <https://doi.org/10.1016/j.flora.2014.03.011>
- De Luis M, Raventós J, Wiegand T, González-hidalgo JC, 2008. Temporal and Spatial Differentiation in Seedling Emergence May Promote Species Coexistence in Mediterranean Fire-Prone Ecosystems. *Ecography* 31: 620-629. <https://doi.org/10.1111/j.0906-7590.2008.05433.x>
- Erfanifard Y, Stereńczak K, 2017. Intra- and interspecific interactions of Scots pine and European beech in mixed secondary forests. *Acta Oecol* 78: 15-25 <https://doi.org/10.1016/j.actao.2016.12.002>
- Erfanifard Y, Nguyen HH, Schmidt JP, Rayburn A, 2018. Fine-scale intraspecific interactions and environmental heterogeneity drive the spatial structure in old-growth stands of a dioecious tree. *For Ecol Manage* 425: 92-99. <https://doi.org/10.1016/j.foreco.2018.05.041>
- Farjon A, 2010. A Handbook of the World's Conifers. Koninklijke Brill NV, Leiden. <https://doi.org/10.1163/9789047430629>
- Fennane M, Ibn Tattou M, Mathez J, Ouyahya A, El Oualidi J, 1999. Flore pratique du Maroc. Pteridophyta, Gymnospermae, Angiospermae (*Lauraceae* - *Neuradaceae*). Travaux de l'Institut Scientifique série Botanique, Agdal, Rabat. 559 pp.
- Gadow K, Zhang CY, Wehenkel C, Pommerening A, Corral-Rivas J, Korol M, Myklush S, Hui GY, Kiviste A, Zhao XH, 2012. Forest Structure and Diversity. In: Continuous Cover Forestry; Pukkala T, Gadow VK, (Eds). Springer Netherlands: Dordrecht, The Netherlands pp 29-83. https://doi.org/10.1007/978-94-007-2202-6_2
- García-Cervigón AI, Velázquez E, Wiegand T, Escudero A, Olano JM, 2017. Colonization in Mediterranean old-fields: the role of dispersal and tree - tree interactions. *J Veget Sci*, 28, 627-638. <https://doi.org/10.1111/jvs.12500>
- Gavrikov V, Stoyan D, 1995. The use of marked point processes in ecological and environmental forest studies. *Environ Ecol Stat* 2: 331-344. <https://doi.org/10.1007/BF00569362>

- Getzin S, Dean C, He F, Trofymow JA, Wiegand K, Wiegand T, 2006. Spatial patterns and competition of tree species in a Douglas-fir chronosequence on Vancouver Island. *Ecography* 29: 671-682. <https://doi.org/10.1111/j.2006.0906-7590.04675.x>
- Getzin S, Wiegand K, Schumacher J, Gougeon A, 2008. Scale-dependent competition at the stand level assessed from crown areas. *For Ecol Manage* 255: 2478-2485. <https://doi.org/10.1016/j.foreco.2008.01.007>
- Ghallab A, Taïqui L, 2015. Modélisation de la distribution spatiale des paramètres bioclimatiques dans la région Tanger- Tétouan (Rif occidental). *Eur Sci J* 11 (17): 265-282
- Goreaud F, Péliissier R, 2003. Avoiding misinterpretation of biotic interactions with the intertype-function: population independence vs. random labeling hypothesis. *J Veget Sci* 14: 681-692. <https://doi.org/10.1111/j.1654-1103.2003.tb02200.x>
- Illian J, Penttinen A, Stoyan H, Stoyan D, 2008. Statistical Analysis and Modelling of Spatial Point Patterns. International Statistical Review. John Wiley, New York, USA. 534 pp. <https://doi.org/10.1002/9780470725160>
- Janík D, Král K, Adam D, Hort L, Samonil P, Unar P, Vrska T, McMahon S, 2016. Tree spatial patterns of *Fagus sylvatica* expansion over 37 years. *For Ecol Manage* 375: 134-145. <https://doi.org/10.1016/j.foreco.2016.05.017>
- Jácome-Flores ME, Delibes M, Wiegand T, Fedriani JM, 2016. Spatial patterns of an endemic Mediterranean palm recolonizing old fields. *Ecol Evol* 6: 8556-8568 <https://doi.org/10.1002/ece3.2504>
- Law R, Illian J, Burslem DFRP, Gratzer G, Gunatilleke CVS, Gunatilleke IAUN, 2009. Ecological information from spatial patterns of plants: Insights from point process theory. *J Ecol* 97: 616-628. <https://doi.org/10.1111/j.1365-2745.2009.01510.x>
- Legendre P, Legendre L, 1998. Numerical Ecology (2nd English edn). Amsterdam, The Netherlands: Elsevier. 853 pp.
- LeMay V, Pommerening A, Marshall P, 2009. Spatio-temporal structure of multi-storied, multi-aged interior Douglas fir (*Pseudotsuga menziesii* var. *glauca*) stands. *J Ecol* 97: 1062-1074. <https://doi.org/10.1111/j.1365-2745.2009.01542.x>
- Linares JC, 2011. Biogeography and evolution of *Abies* (*Pinaceae*) in the Mediterranean Basin: The roles of long-term climatic change and glacial refugia. *J Biogeogr* 38: 619-630. <https://doi.org/10.1111/j.1365-2699.2010.02458.x>
- Linares JC, Camarero JJ, Carreir JA, 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. *J Ecol* 98: 592-603. <https://doi.org/10.1111/j.1365-2745.2010.01645.x>
- Linares JC, Carreira JA, Ochoa V, 2011. Human impacts drive forest structure and diversity. Insights from Mediterranean mountain forest dominated by *Abies pinsapo* (Boiss.). *European J For Res* 130: 533-542. <https://doi.org/10.1007/s10342-010-0441-9>
- Loosmore NB, Ford ED, 2006. Statistical inference using the g or k point pattern spatial statistics. *Ecology* 87: 1925-1931. [https://doi.org/10.1890/0012-9658\(2006\)87\[1925:SIUTGO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2)
- Médail F, Diadema K, 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. *J Biogeogr* 36: 1333-1345. <https://doi.org/10.1111/j.1365-2699.2008.02051.x>
- Melhaoui Y, 1990. Etude phytoécologique, productivité et classes de croissance du Sapin du Maroc (*Abies maroccana* Trab.). Problématique de la régénération naturelle des peuplements de la sapinière marocaine. Doctoral thesis, Aix-Marseille III Univ, Aix-Marseille, France.
- Motta R, Edouard JL, 2005. Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley, Piedmont, Italy. *Can J For Res* 36: 21-36. <https://doi.org/10.1139/x04-153>
- Navarro-Cerrillo RM, Manzanedo RD, Rodriguez-Vallejo C, Gazol A, Palacios-Rodríguez G, Camarero JJ, 2020. Competition modulates the response of growth to climate in pure and mixed *Abies pinsapo* subsp. *Maroccana* forests in northern Morocco. *For Ecol Manage* 459: 117847. <https://doi.org/10.1016/j.foreco.2019.117847>
- Raventós J, Wiegand T, De Luis M, 2010. Evidence for the spatial segregation hypothesis : a test with nine-year survivorship data in a Mediterranean shrubland. *Ecology* 91: 2110-2120. <https://doi.org/10.1890/090385.1>
- Raventós J, Mujica E, Wiegand T, Bonet A, 2011. Analyzing the Spatial Structure of *Broughtonia cubensis* (*Orchidaceae*) Populations in the Dry Forests of Guanahacabibes, Cuba. *Biotropica* 43: 173-182. <https://doi.org/10.1111/j.1744-7429.2010.00684.x>
- Ripley BD, 1977. Modelling Spatial Patterns. *Journal of the Royal Statistical Society* 39: 172-212. <https://doi.org/10.1111/j.2517-6161.1977.tb01615.x>
- Sánchez-Salguero R, Camarero JJ, Carrer M, Gutiérrez E, Alla AQ, Andreu-Hayles L, Hevia A, Koutavas A, Martínez-Sancho E, Nola P, *et al.*, 2017. Climate extremes and predicted warming threaten Mediterranean Holocene fir forests refugia. *Proceedings of the National Academy of Sciences of the United States of America* 114: 10142-10150. <https://doi.org/10.1073/pnas.1708109114>
- Schall P, Schulze ED, Fischer M, Ayasse M, Ammer C, 2018. Relations between forest management, stand

- structure and productivity across different types of Central European forests. *Basic App Ecol*: 32: 39-52. <https://doi.org/10.1016/j.baae.2018.02.007>
- Sękiewicz K, Sękiewicz M, Jasińska AK, Boratyńska K, Iszkuło G, Romo A, Boratyński A, 2013. Morphological diversity and structure of West Mediterranean *Abies* species. *Plant Biosyst* 147: 125-134. <https://doi.org/10.1080/11263504.2012.753130>
- Stoyan D, Stoyan H, 1994. Fractals, random shapes and point fields. *Methods of geometrical statistics*. John Wiley & Sons, Chichester, UK. 394 pp.
- Szmyt J, 2014. Spatial statistics in ecological analysis: From indices to functions. *Silva Fennica* 48: 1-31. <https://doi.org/10.14214/sf.1008>
- Taïqui L, 2005. Evolution récente de la structure du paysage du Bassin de Chefchaouen (1958-1986). *Mutations Des Milieux Ruraux Dans Les Montagnes Rifaines (Maroc), Série Etudes Spatiales* 2: 1-19.
- Velázquez E, Martínez I, Getzin S, Moloney KA, Wiegand T, 2016. An evaluation of the state of spatial point pattern analysis in ecology. *Ecography* 39: 001-014. <https://doi.org/10.1111/ecog.01579>
- Wiegand T, Gunatilleke S, Gunatilleke N, 2007. Species Associations in a Heterogeneous Sri Lankan Dipterocarp Forest. *Am Nat* 170: E77-E95. <https://doi.org/10.1086/521240>
- Wiegand T, Moloney KA, 2014. *Handbook of Spatial Point- Pattern Analysis in Ecology*. Chapman and Hall/CRC Press, Boca Raton, FL. 212-234 pp. <https://doi.org/10.1201/b16195>
- Wiegand T, Moloney KA, 2004. Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 2: 209-229. <https://doi.org/10.1111/j.0030-1299.2004.12497.x>
- Zenner EK, Peck JE, 2009. Characterizing structural conditions in mature managed red pine: Spatial dependency of metrics and adequacy of plot size. *For Ecol Manage* 257: 311-320. <https://doi.org/10.1016/j.foreco.2008.09.006>
- Zhang C, Wei Y, Zhao X, Gadow KV, 2013. Spatial characteristics of tree diameter distributions in a temperate old-growth forest. *PLoS ONE* 8:e58983. <https://doi.org/10.1371/journal.pone.0058983>