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Environmental and anthropogenic drivers of coniferous species distribution in Mediterranean drylands from North West Algeria

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Abstract:	Understanding the influence of environmental and anthropogenic factors on the distribution of species is essential for developing management in endangered ecosystems. We studied the current abundance and distribution patterns of vegetation along environmental and anthropogenic gradients by shaping their distribution in North West Algeria. We put special emphasis in the four dominant coniferous species (Pinus halepensis, Tetraclinis articulata, Juniperus oxycedrus and Juniperus phoenicea). We compiled inventories of species composition, together with 12 environmental variables in 177 sampling plots throughout the study area. Multivariate and univariate analyses were applied to predict presence of coniferous species and to explore species-environment relationships along ecological and anthropogenic variables. We found that species segregated along environmental gradients, mainly altitude and related climatic variables (temperatures). Anthropogenic variables, like fire frequency and overgrazing, were secondary, but also significant. J. phoenicea was located exclusively in coastal areas. T. articulata had a wide distribution and was linked to coastal and inland areas, but did not arrive at more continental areas (colder and drier), where it was replaced with J. oxycedrus. P. halepensis displayed the widest distribution and was practically present throughout the study area, but its maximum distribution was in continental areas. These results indicate a possible shift of species' potential distribution in future climatic change. Species like J. oxycedrus would be seriously threatened by niche narrowing, while P. halepensis and T. articulata could expand to a certain extent. Our results provide important inputs for optimising the management plans of coniferous species by considering environmental factors key modulators of vegetation distribution.
Response to Reviewers:	Title: Environmental and anthropogenic drivers of coniferous species distribution in Mediterranean drylands from North West Algeria Folia Geobotanica

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Please find enclosed a copy of our revised manuscript in which address suggestions of Reviewer #1:

QUESTION: I have now checked the manuscript and I am happy to read that the authors have addressed all my comments. I think that the paper the manuscipt can be accepted but I would like to draw their attention to the following perhaps minor issues.
RESPONSE: Thanks!

QUESTION: One of my earlier comments was: Please place the study area in the context of Algeria by providing some information on species and biogeography.

By that I meant give concise info on the number of flora in Algeria the endemism level and the chorology of the flora and then suggest how the flora of your study area compares to that of the country. This is important background info for the reader which can be summarised in 5 lines. Not much work for the authors really

RESPONSE: Following the Reviewer's suggestion we have included some references about the North African and Algerian flora (number of species and endemism). Then we compare these values with the flora in our study site. As the Reviewer suggests, this can help the reader to understand our study. See lines 123-130.

QUESTION: Regarding the localization map (Fig1) the authors provide major geomorphologic zones on the legend not places names. I don't think that by adding 3-4 major place names the figure would get overloaded. Algeria is a large country and its geography unfortunately is not well-known to the average reader.

RESPONSE: We have modified Fig. 1. We have included three of the main cities in the study area. As the Reviewer suggests, this can help to put in situation our readers.

We would like to thank again the Reviewers and the Editor for the time dedicated to our manuscript and for their numerous, constructive and helpful comments provided. We also feel that the manuscript has substantially improved with the changes introduced, and hope that this new version will be suitable for publication in Folia Geobotanica.
Sincerely,
M. Jaime Baeza.

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Environmental and anthropogenic drivers of coniferous species distribution in Mediterranean drylands from North West Algeria

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Dedicated to Faouzia Ayache (Nedroma, 1976–2016).

Abstract

Understanding the influence of environmental and anthropogenic factors on the distribution of species is essential for developing management in endangered ecosystems. We studied the current abundance and distribution patterns of vegetation along environmental and anthropogenic gradients in North West Algeria. We focused on the four dominant coniferous species (*Pinus halepensis, Tetraclinis articulata, Juniperus oxycedrus* and *Juniperus phoenicea*). We compiled inventories of species composition, together with 12 environmental variables in 177 sampling plots throughout the study area. Multivariate (Detrended Correspondence Analysis) and univariate (HOF models) analyses were applied to predict presence of coniferous species and to explore species-environment relationships along ecological and anthropogenic variables. We found that species segregated along environmental gradients, mainly altitude and related climatic variables (temperatures). Anthropogenic variables, like fire frequency and overgrazing, were secondary, but also significant. *J. phoenicea* was located exclusively in coastal areas. *T. articulata* had a wide distribution and was linked to coastal and inland areas, but did not arrive at more continental areas (colder and drier), where it was replaced with *J. oxycedrus*. *P. halepensis* displayed the widest distribution and was practically present throughout the study area, but its maximum abundance was in continental areas. These results indicate a possible shift of species' potential distribution in future climatic change. Species like *J. oxycedrus* would be seriously threatened by niche narrowing, while *P. halepensis and T. articulata* could expand to a certain extent. Our results provide important inputs for optimising the management plans of coniferous species by considering environmental factors key modulators of vegetation distribution.

Keywords: coniferous forest, fire frequency, global change, overgrazing, species distribution gradient.

1. Introduction

In recent years, predictive modelling of species distribution has become an important tool to address ecology and biogeography issues (Franklin 2010; Acevedo et al. 2012) and, more recently, in restoration, conservation biology and climate change research (Hannah et al. 2014). In ecological studies, species-environment relationships have been crucial for explaining the spatial structuring of natural ecosystems (Davies et al. 2007). It is essential to determine the interactions between abiotic factors that limit species existence (fundamental niche) with anthropogenic and other biotic factors constraining this existence (realized niche) (Pearman et al. 2008). Co-existing tree species have different responses to environmental factors, determined by their genetic and physiological features, as well as their relationships to physiochemical variables (fundamental niche). However, interactions with other organisms, selective management, and human-induced disturbances can vastly alter these potential plant-environment patterns (realized niche) (Nicolaci et al. 2015). Many studies relate present-day geographic distributions to climatic variables (Pliscoff et al. 2014), and then project future distributions in various climate change scenarios (Boden et al. 2010). Furthermore, climate in combination with other environmental factors, such as soil and elevation (Nicolaci et al. 2015), natural and human disturbances (e.g., fire; Baeza et al. 2007) and historical management (Urbieta et al. 2011), has been much used to explain the main vegetation patterns around the world (Schwilk and Keeley 2012). Therefore, accurate knowledge of the ecological and anthropogenic drivers that affect vegetation distribution is necessary for forest planning and for designing models of species distribution (Hörsch 2003). This information would be particularly important in the conservation of endangered ecosystems, such as some coniferous forests in the Mediterranean Basin (Rupprecht et al. 2011).

Under the arid and semiarid climatic conditions that exist in the Mediterranean Basin, coniferous forests are a substantial component, with taxa of pine (to a greater extent) and cupressaceous species (to a lesser extent) found among the most dominant elements (Quézel 2000). These woodlands are of enormous ecological and economic importance since they contribute significantly to local economy, and also because of their relevance for regional biodiversity (Médail 2003) that enhances large-scale ecosystem multifunctionality (van der Plas et al. 2016). Coniferous forest distribution in Mediterranean landscapes is characterised by occupying diverse environmental conditions in relation to climate and soils, and by the frequency and intensity of disturbances (both natural and anthropogenic) (Le Houerou 1980). However, the socio-economic differences between Northern and Southern Mediterranean countries lead to different ecological and anthropogenic pressures (Chergui et al. 2018). In

Northern countries, for example, rural depopulation has promoted the expansion of conifer species and forests (mainly *Pinus halepensis*) in the last decades (Quézel 2004). In this case, fire occurrence is the main degradation factor as consequence of the increasing amount and connectivity of fuels (Santana et al. 2010; Chergui et al. 2018). In contrast, Southern countries have a sizeable rural population growth combined with a predominantly precarious way of life (Zohry 2005). In this case fire is not the predominant degradation factor and the overexploitation of natural resources by means of agriculture, wood gathering and grazing can also be a source of degradation (Taïqui and Martin, 1997; Hadjadj Aoual 2009). In Algeria, forests have historically been subjected to disturbances, but the deforestation threat has increased in recent times as these disturbances have intensified (Dahmani-Megrerouche 2002; Hadjadj Aoual 2009). In fact, the strong human pressure on Algerian forests has diminished their extent and has changed their structure to shrublands, croplands and grasslands. Nevertheless, some specific forest types, in particular those dominated by the coniferous ones, still persist and are of conservation interest (Hadjadj Aoual 2009). Despite their considerable value, very little information on the spatial distribution of these coniferous species is available, which may hamper future conservation planning. Previous studies in north west Algeria (Dahmani-Megrerouche 2002; Hadjadj Aoual 2009; Kadik 2011) have facilitated the characterisation of the structure and floristic composition of vegetation, including coniferous formations. However, no study has attempted to assess the habitat distributions of these species along environmental gradients. Such an assessment would undoubtedly help to implement adequate conservation and sustainable development programmes to protect these endangered systems. Despite the threatened status of many coniferous species that require attention, many questions about their biogeography and ecology still remain unsolved.

The present study analyses the factors that drive the distribution patterns of four coniferous species in an arid area from North West Algeria. We focused on this area because it includes a smooth biome transition between Mediterranean and arid climatic conditions, and is characterised by great climatic complexity, altitude and distance from the Mediterranean Sea. Coniferous woodland constitutes the most widely distributed vegetation types of drylands in the southern Mediterranean Basin, and studying this area can provide insights for future management plans. We focused on investigating the relationships between the abundance of these species and various key environmental (climatic and geomorphic) and anthropogenic (fire and grazing) factors. The quantification of such species-environment relationships represents the core of predictive geographical modelling in ecology (Thuiller et al. 2003). This assessment is essential for improving the use of coniferous species in afforestation programmes where their presence is endangered. To this end, it is fundamental to study the environmental factors that determine the ecological niche of these species. Specifically this work aimed to answer three questions: (1) what is the current distribution of four dominant coniferous species along the environmental gradients in North West Algeria? (2) which environmental variables prove the most important in predicting coniferous species distribution? (3) do anthropogenic-caused disturbances, such as grazing and fire, influence species distribution?

2. Material and methods

2.1 Study area

About 4000 plant species occur in the north African of the Mediterranean region. Of these, approximately 72 % are Mediterranean endemics, though only 20% are confined to North Africa (White 1983). Algeria includes most of this flora with 3139 species (RNE 2000). The study area is located in North West Algeria, Wilaya of Tlemcen (Fig 1), whose geomorphology reveals a wide diversity of landforms, including from north to south: coastal area, the mountains of Traras, the Tellians plains, the mountains of Tlemcen and a pre-steppe area (Fig 1). Most of this area is composed mainly of degraded and disturbed vegetation dominated chiefly by coniferous species (e.g., *P. halepensis*, *Tetraclinis articulata*, *Juniperus oxycedrus* and *Juniperus phoenicea*.). In this sense, these species and the companion flora accounts approximately 10% of Algerian flora (Ayache 2007).

The area encompasses a wide elevation range from sea level to 1,180 m, characterised by an arid and semiarid climate with wide inter-annual variability. Mean annual temperatures range from 13ºC to 20°C, and annual mean rainfall varies between 254 mm and 484 mm (The National Office of Meteorology, the 1980-2011 period). A detailed description of the study sites is provided in Table 1. In the study area, the wide spatial variation of the key environmental factors, as well as the heterogeneity that arises from human-produced disturbances, lead to a diverse mosaic of Mediterranean vegetation. This mosaic is composed of degraded vegetation dominated by these four coniferous species (*P. halepensis*, *T. articulata*, *J. oxycedrus* and *J. phoenicea*. Only a few of these coniferous-dominated forests remain intact, and are sometimes mixed with evergreen oaks (*Quercus ilex* and *Quercus suber*). The most common accompanying shrubs are: *Quercus coccifera, Pistacia lentiscus*, *Rosmarinus officinalis, Olea europea*, *Phillyrea angustifolia, Erica multiflora*, *Cistus ssp.,* and some other communities of halophytes and psammophytes. This area has also been historically subjected to intense disturbances, e.g. overgrazing and recurrent fires, which have led to a major deforestation threat in recent times (Meddour-Sahar 2015). Species nomenclature used in this study is based on Quezel and Santa (1962-63).

The forested area occupies around 199,488 ha of a total study area that covers 901,769 ha, of which 115,500 ha are dominated by coniferous species (58% of the forested area, DGFT, 2011). In this study, we focused on the distribution of the four coniferous species that are dominant in the study area: *P. halepensis*, *T. articulata*, *J. oxycedrus* and *J. phoenicea.*

2.2 Sampling design

Sampling was designed by considering distance from the sea, different altitudes, and presence and dominance of coniferous species (Fig 1, Table 1). Sampling also included vegetation types, where *Q. ilex* and *Q. suber* are present. Along a latitudinal transect from the coast to the pre-steppic area, 14 sites were selected as study sites, which represented the main coniferous forests for the different altitudes, aspects and substrata (Table 1). At each site, 10 to 22 plots were established randomly depending on space availability; e.g., the number of plots per site was proportional to the total area occupied by coniferous species. Vegetation sampling was conducted in the springs of 2008 and 2009 following the phytosociological method of Braun Blanquet (1952). A list of all the species present in an area of 100 m^2 was collected per plot. This sampling size has been considered sufficient to properly record the vegetation in our study area (Hadjadj Aoual 1995). For each plot, all the vascular species present were annotated and accompanied with an abundance-dominance index (Braun Blanquet 1952). Subsequently, the coefficients of abundance-dominance (on the 6-level scale of Braun Blanquet: +, 1, 2, 3, 4, 5) were transformed to a cover percent (0.1%, 5%, 17.5%, 37.5%, 62.5% and 87.5%) with the conversion proposed by van der Maarel (1979). The floristic composition and environmental characteristics were sampled in 177 plots distributed among the 14 sites.

2.3 Explanatory variables

Twelve environmental variables were considered as being explanatory for species distribution. For each plot we measured: altitude, distance from the sea, vegetation cover, slope, aspect, precipitations, the minimum temperature of the coldest month, snow, continentality and substratum type. Fire and grazing frequency were also included as anthropogenic explanatory variables. Altitude was extracted from the Z coordinate of the GPS in the field. Distance from the sea was determined from the map created by gvSIG [http://www.gvsig.org; last accessed October 2015]. Vegetation cover was considered as the percentage of vascular species coverage. Slope and aspect (north, east, west and south) were determined in the field using a clinometer and a compass. We obtained climate data from the records of the nearest weather stations; mean annual precipitations, annual minimum temperatures and annual average of days with snowing days. Climate data encompassed the period from 1980 to 2011. Continentality was estimated according to Debrach's Index (Debrach, 1953). This index calculates the difference between the mean daily maximum temperature of the warmest month (M) and the mean daily minimum temperature of the coldest month (m) (°C). According to this index, when M-m < 15°: Island climate, 15°C < M-m < 25°C: Coastal climate, 25°C < M-m < 35°C: semi-continental climate, M-m > 35°C: continental climate. For clarity in the data analysis, some variables were semi-quantitatively classified. Aspect was classified following an increasing gradient of aridity from 1 to 4 (1: north, 2: east, 3: west, 4: south) (Baeza et al. 2007). Disturbance caused by grazing was estimated by visual evidence, the information provided by local people and the statistics of forest services (DGFT 2011). Three grazing levels were established: 0: absent, 1: frequent, 2: overgrazing. Fire occurrence was expressed as: 0: absent, and 1: present, where plots were classified according to evidence of past fire recorded during the 1987-2011 period by the forest conservation services of Tlemcen (DGFT 2011). Soil substratum was classified as: siliceous (1) or limestone (2). As expected, climatic variables related to temperature (minimum temperature, snow and the Debrach index) were correlated among them, as well as with distance from the sea and altitude (Table S1). Therefore, in subsequent analysis we used only elevation as descriptor of all these variables for simplicity.

2.4 Data analysis

The collected data yielded a matrix of 177 plots and 192 vascular species. These data were analysed by means of ordination methods to describe patterns in species composition and vegetation types in relation to the environmental and anthropogenic characteristics. For this purpose we used the "vegan" package for multivariate analyses (Oksanen et al. 2015) within the R software environment (R Development Core Team 2015, v. 3.2.2, Vienna, Austria). Firstly, vegetation data were analysed by a detrended correspondence analysis (DCA; Hill and Gauch 1980), where cover values were log(x+1) transformed and rare species were downweighted to fraction 5. Secondly, once the DCA analysis was performed, we distinguished different community types by means of a hierarchical cluster analysis of the two first axes of the sampled plots scores of the DCA (Orlóci 1978). These community types would be initially dominated by different combinations of the studied coniferous species. Thirdly, to determine the relationship of environmental variables sampled on species composition, we fitted these variables passively into the species ordination space (passive fit: function "envfit" with 1000 permutations). Aspect, grazing, fire occurrence, soil substratum were included in the passive analysis as semi-quantitative variables for obtaining more visual results. Finally, the response of the four studied coniferous species was modelled according to the continuous environment variables by means of Huisman-Olf-Fresco (HOF) models (Jansen and Oksanen 2013). HOF models are a means of describing species response to environmental gradients. A hierarchical series of seven response models are fitted, ranked by their increasing complexity (Model I, no species trend; Model II, increasing or decreasing trend; Model III, increasing or decreasing trend below a maximum attainable response; Model IV, symmetrical unimodal response curve; Model V, unimodal skewed response curve; Model VI, response with two unimodal equal optima; and VII, response with two unimodal unequal optima. These models were fitted using a Gaussian error distribution, and the model with higher parsimony (lower Akaike's information criterion, AIC) was selected. For categorical variables fire, grazing and substratum, the mean and the 95% confidence intervals were estimated by the means of bootstrapping with 999 bootstrap replicates. HOF models were fitted with the "eHOF" package (Jansen and Oksanen 2013) within the R environment, while bootstrapping was performed by means of the "boot" package (Canty and Ripley 2017).

3. Results

3.1 Multivariate analysis for community composition.

A total of 192 species were detected in the whole study (Table S2). Vegetation cover in the sampled plots averaged 52%, but ranged from 30% to 70%. The DCA analysis produced eigenvalues (λ) of 0.42, 0.38, 0.28, 0.28 and gradient lengths of 3.99, 3.97, 3.95 and 2.83 for the first four axes. The cluster analysis on the sample-plots scores from the first two axes of the DCA (Fig 2) determined four different community types (Fig 3a). All environmental variables analysed showed a significant relationship with the DCA 1 or DCA 2 axes (Table 2, Fig 3b).

A first community type (C1) was ordinated on the lower left-hand side of the DCA plot. C1 was placed at low elevation sites, with short distances from the sea and low continentality (Fig 3a). This community was dominated mainly by *J. phoenicea*, accompanied by shrub species such as *Erica multiflora* and *Pistacia lentiscus* (Fig 3c). A second community type (C2) was also ordinated in the lower left-hand side of the DCA, but at less negative values of DCA 2. This community was also placed at low elevation sites, but it was affected by a higher grazing pressure. C2 was composed mainly by *Tetraclinis articulata*, accompanied by *Chamaerops humilis*, *Lavandula dentata*, *Cistus monspelliensis* and *Rosmarinus officinalis*. A third community type (C3) was observed at intermediate values of altitude, which in addition experienced the highest levels of pasture and southern aspects. This community type was dominated by *Tetraclinis articulata* with an important presence of *Ceratonia siliqua*, *Cistus albidus*, *Olea europaea* and *Cistus ladaniferus*. Herbaceous species, such as *Bromus rubens* and *Plantago lagopus,* also acquired relevance in C3 composition. Finally, there was depicted a fourth community type (C4) which occupied sites with the highest elevation and precipitation levels. This community was dominated by *Pinus halepensis* and *Juniperus oxycedrus*, accompanied by *Quercus ilex, Quercus coccifera*, *Phillyrea angustifolia*, *Globularia alypum* and *Cistus villosus*. Grasses as *Stipa tenacissima* and *Ampelodesmos mauritanica* were also present in C4.

3.2 HOF models for coniferous species.

The response to the altitude gradient showed that *P. halepensis* was the most widely represented, but was in lower (0-200 m) and higher areas (>1,000 m) where its full development was found (Fig 4). *J. phoenicea* occupied low land areas (>250 m), whereas *T. articulata* occupied a fringe between the coast and 400 m. *J. oxycedrus* showed an asymptotic response with its optimum value starting from 800 to 1,200 m.

The precipitation gradient showed that *P. halepensis* had a wide rainfall range. This species comprised areas of annual rainfall between 250 and 500 mm, with its optimum in the areas within the 350-450 mm range (Fig 4). The optimum of *T. articulata* was below *P. halepensis* (around 350 mm), and *J. phoenicea* did not follow any pattern regarding to precipitation. The maximum response of *J. oxycedrus* was obtained in the wettest zone of the study area (> 400 mm), below which it was scarce, but could withstand arid areas with 300-350 mm.

P. halepensis and *J. oxycedrus* were the species distributed most frequently on the steepest slopes (Fig 4), whereas *J. phoenicea* was the species that occupied the flattest environments. *T. articulata* was found at intermediate slopes (15-25°). *J. oxycedrus* was the species favoured xeric aspects (south and west) (Fig 4). In contrast, *J. phoenicea* displayed more affinity to northern aspects. *P. halepensis* showed affinity for eastern and western aspects, whereas any affinity was observed for *T. articulata*.

Fire diminished the presence of *J. oxycedrus* and *P. halepensis*, but increased that of *T. articulata* and *J. phoenicea* (Fig 5a). Overgrazing had a negative impact on all species responses, but intermediate grazing promoted their response in *J. phoenicea* and *T. articulata* (Fig 5b). Finally, *J. phoenicea* showed more affinity for siliceous substratum than for limestones (Fig 5c).

4. Discussion

4.1 Environmental and anthropogenic vegetation drivers

Coniferous species and their associated communities segregate mainly along the altitudinal gradient depicted for our study in North West Algeria, a gradient that is highly correlated to continentality (distance to the sea). This is in accordance with other studies into coniferous formations (Boden et al. 2010; Rupprecht et al. 2011; Urbieta et al. 2011; Serra-Diaz et al. 2013; Nicolaci et al. 2015), which have shown that both degree of continentality and altitude are the two environmental factors that strongly modulate coniferous vegetation distribution. Similarly, other vegetation types have also been limited by these gradients (Sanders et al. 2014).

Continentality was one of the main controlling factors for vegetation growth and distribution in our study. In fact, in coastal areas, with lower thermal amplitude where snow is an exceptional phenomenon, the shrublands of *J. phoenicea* were abundant, but well-localised. These maritime *Juniperus* strongly compete with more widespread species; e.g. *P. halepensis* and *T. articulata.* Indeed the coastal area is occupied mainly by this community type where *P. halepensis* and *T. articulata* are also present. It is worth noting that *P. halepensis* forests have been widely promoted by extensive plantation along the coast in Algeria since the 20th century (Kadik 2011), which would partially explain the wide distribution of this species. After this initial coastal vegetation type, the landscape went on to be dominated by *T. articulata*. This species avoids sand dunes where salt spray has damaging effects and gives way to *J. phoenicea*, which is more resistant (Fennane and Barbero 1984). *T. articulata* was found to be related to coastal and semi-continental areas because the effects of prolonged winter frosts in the more continental areas eliminates this species, which is relegated by *J. oxycedrus* and *P. halepensis* that better tolerate these conditions (Hadjadj Aoual 1995; Dahmani-Megrerouche 2002). Thermophyllus species like *P. lentiscus* and *C. humilis* (Baeza et al. 2007) were also found in the lower areas accompanying these community types dominated by either *J. phoenicia* or *T. articulata*. Distance from the sea generates a cooler climate suitable for *J. oxycedrus* and *P. halepensis* occurrence, and eliminates *T. articulata* and the maritime *J. phoenicea.* The optimum of *J. oxycedrus* occurs under these conditions, and can be mixed with *Q. ilex*, *Q. coccifera* and *P. angustifolia* (Dahmani-Megrerouche 2002). These results are interesting because they denote that climatic factors other than aridity (precipitation) play a preponderant role in vegetation distribution in drylands. In our study, precipitation had some effect on coniferous distribution, but was less important compared to temperature factors (altitude and the correlated minimum temperature, Debrach's Index, snow). *P. halepensis* displayed a relative wide annual precipitation range, whereas *J. phoenicea* did not show any precipitation effect.

Despite these two factors (altitude and precipitation) being the most important, geomorphological variables (aspect and slope) also influence vegetation distribution locally (Baeza et al. 2007); e.g., *J. oxycedrus* was the species that better supported xeric aspects (south and west), whereas *J. phoenicea* displayed more affinity to northern aspects. Similarly, *J. oxycedrus* was able to withstand the highest slopes, while *J. phoenicea* preferred flat environments. These results are in accordance with other studies performed in different Mediterranean communities (Carmel and Kadmon 1999; Sternberg and Shoshany 2001), where geomorphological variables are determinant.

The current distribution patterns of coniferous species in our study area are largely defined by environmental variables but anthropogenic activity, as grazing and fire, also affect in some way vegetation composition. This finding agrees with those found by recent studies, which have examined the relationship between species occurrence and species' ability to recover after disturbances (Màrcia et al. 2006; Angert et al. 2011). Indeed in our study area, which is affected by irregular grazing and recurrence fire, we observed that vegetation corresponds to fire-prone shrub communities and mixed scrubland in different degradation stages (with the significant presence of *T. articulata*). Many plant species in highly disturbed areas have life-history traits that determine their post-fire establishment patterns (Syphard and Franklin 2010); e.g., the fire-surviving strategy of *P. halepensis* is characterised by its stand resilience and its post-fire seeding from serotinous cones, while *T. articulata* adapts a post-fire dual strategy by both resprouting and seedling germination from soil seed banks (López Hernández et al. 1995). This could have favoured these two species in fire-prone areas over the maritime *J. phoenicea* species, which show lower post-fire survival (Rupprecht et al. 2011). Fire has a contrasting effect on species according to its intensity and frequency. High fire frequency might limit the presence of *P. halepensis*, but promotes *T. articulata* (Màrcia et al. 2006). It is well-known that *P. halepensis* regenerates well after fire, but its regeneration can be threatened if the time between fires is shorter than the time needed to replenish its seed bank (Baeza et al. 2007). We also found accompanying shrubs typical of vegetation types resulting from fire recurrence; e.g., *Cistus albidus*, *C. monspelliensis*, *C. ladanifer*, *E. multiflora* and *R. officinalis* (Santana et al. 2010). These are seeding species characterised by a persistent soil seedbank that experience a flush of germination and establishment after fire (Santana et al. 2013). It is noteworthy that we found the maximum *J. phoenicea* distribution in areas where fire is present, despite this species being considered poorly fire-resilient (Lloret and Vilà 2003). This species does not regenerate by either resprouting or seeding after fire, but its regeneration depends on bird-dispersed seeds from unburned patches (Lloret and Vilà 2003). This is surprising, but could be explained by the coincidence of its optimal habitat with the area where anthropogenic fires are more frequent (i.e., close to the sea where the population is larger). If fires are not large and catastrophic in dimension, this species may persist by colonising from neighbouring unburned patches. Finally, grazing pressure was also a determinant factor in vegetation composition. Overgrazing decreased the presence of all coniferous species studied; however, grazing at intermediate values enhanced *J. phoenicea* and *T. articulata*. Some herbaceous species like *B. rubens* and *P. lagopus* were also favoured by this disturbance. This results are in line with "Intermediate Disturbance Hypothesis" (Connell, 1978), where too little disturbance leads to low diversity through competitive exclusion and too much disturbance eliminates species incapables of rapid re-colonization (Wilkinson 1999). Therefore, it is important to be able to estimate the thresholds under which grazing may be applied without causing degradation, taking also into account that it can synergistically act as degradation factor in combination with fire (Calvo et al. 2012). For example, it is well documented in other Mediterranean countries, such as Greece and Israel, that fire is used by shepherds as a tool for improving pasture lands (Perevolotsky et al. 2002; Papanastasis 2004). However, the abuse of this technique can lead to soil and vegetation degradation problems (Calvo et al. 2012). It is fundamental, thus, to ascertain if these anthropic degradation loops are present in Algerian ecosystems as well as to design sustainable management actions.

It should be borne in mind that the present coniferous distribution may sustain modifications in future climate scenarios, where warmer and drier environmental conditions are predicted for the Mediterranean Region (IPCC 2014). Future warming and less rainfall may affect the vegetation in this region and displacements will probably take place, but also because forest fires are likely to intensify (Angert et al. 2011). The range of the studied coniferous species is predicted to intensely and rapidly reduce, and will probably migrate in both altitude and latitude (Keenan et al. 2011). The species with the most continental distribution, e.g., *J. oxycedrus,* would be seriously threatened by niche narrowing. However, those with narrower continental ranges (*P. halepensis and T. articulata*) might be capable of maintaining some of their distribution area, and even with a certain degree of expansion (Esteve-Selma et al. 2012). This is in line with a study performed about the distribution of Iberian tree species, which predicted that *P. halepensis* would be capable of increasing its occupied area in 2020 (Benito Garzón et al. 2008).

4.2 Management implications

Coniferous distribution in drylands is affected by both ecological and anthropogenic factors. Climate is the main driver of the studied coniferous species, while geomorphic gradients (slope) and disturbance (fire and grazing) are secondary, but important. The complexity of the inter-relations between these factors and coniferous species demands further research, including long-term monitoring, to assess the vegetation dynamics and transitions from one vegetation type to another. The relict coniferous forests in the southern Mediterranean Basin are subjected to deforestation as a result of anthropogenic pressure, and *in situ* conservation is hence required. This research establishes that most coniferous species (*T. articulata, J. oxycedrus* and *J. phoenicea*) are characterised by very disjunctive areas. This regional distribution is known in only a few areas of Algeria and the Mediterranean Basin, and therefore highlights the importance of this study to be extrapolated to other degraded areas. In fact, regression in the availability of these species' natural habitat has led them to be considered endangered in Algeria. For this reason, protection by proper legislation of these species and associated ecosystems in Algeria, along with the development of effective management plans, should be made a priority. Unfortunately in the present-day, these species do not occupy a prominent place in forestry interventions as ongoing projects in this region focus mainly on *P. halepensis,* which have shown a low success rate, or even centre on species that are not native to the Mediterranean Basin (*Eucalyptus*, sp, *Cupressus* sp.). Our results could be used to propose management guidelines for the conservation of locally threatened coniferous species and to encourage their reforestation. In short, we describe optimal environmental conditions and areas to develop these management plans for each individual species. Our study also shows that vegetation drivers may differ between Northern and Southern Mediterranean countries. While in Northern countries fire is an important degradation factor (Santana et al. 2010), in the case of Northern Algeria other factors related to the overexploitation of natural resources such as intense agriculture, wood gathering and grazing can also be a source of degradation (Taïqui and Martin, 1997; Hadjadj Aoual 2009).

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TABLES:

Table 1. Study sites in North West Algeria ordinated depending on distance to the Mediterranean Sea. The table includes a description of sampling sites, including: Alt: altitude, DS: distance from the sea, VC: vegetation cover, Slp: slope, Asp: aspect (1: north, 2: east, 3: west, 4: south); P: average annual precipitation, M: minimum temperature of the coldest month, Sn: snow (0: absent, 1:1-3 days, 2: 3-7 days, 3: >7 days), DI: Debrach’s index, Fire (0: absent, 1: frequent), Graz: Grazing (0: absent, 1: frequent, 2: overgrazing), Sub: substratum (1: siliceous, 2: limestone).

Site	Alt (m)	DS (km)	VC (%)	Slp (º)	Asp	P (mm)	M (ºC)	Sn (days y^{-1})	DI (ºC)	Fire	Graz	Sub
Rechgoun	190	0.02	40	10	1	350	10.04	0	21.21	1	1	1
Beni saf	150	0.2	30	15	1	350	10.04	0	21.21	0	2	1
Marsat Ben M'hidi	80	0.6	60	25	1	340	10.93	0	19.57	1	1	1
Ghazaouet	190	2.7	70	20	4	332	8.4	1	24.12	1	1	1
Honaine	100	4.2	40	15	2	350	7.9	1	21.9	0	1	2
OuedSbaa	300	11.8	70	25	1	360	6.26	1	19.94	1	1	1
Nedroma	480	12.4	50	15	1	380	6.12	2	21.08	1	1	1
Maghnia	370	29.5	30	25	2	288	1.92	1	34.3	1	2	2
Hafir	1160	46	70	30	4	484	3.2	3	28.7	1	0	1
Tlemcen	1050	48	70	35	1	460	4.8	3	29.4	0	0	2
OuedLakhdar	800	55.5	50	20	1	320	4.4	2	32.6	0	2	2
OuledMimoun	710	60.5	40	15	2	254	4.2	2	34.8	1	2	2
Sebdou	1130	70	40	15	3	295	2.6	3	28.1	0	2	1
OuedSlissen	1180	73	50	25	3	316	3.5	2	28.7	1	1	1

Table 2. Environmental variables fitted passively to the two first axes of the DCA ordination. Correlation with the first two axes, squared correlation coefficient (R^2) and *P*-value are shown for each variable.

Variables	**DCA 1**	**DCA 2**	**R^2**	***P***
Grazing	-0.191	0.981	0.18	<0.001
Elevation	0.981	0.191	0.55	<0.001
Slope	0.999	0.038	0.08	0.002
Fire	-0.977	-0.212	0.13	<0.001
Precipitation	0.880	-0.475	0.09	<0.001
Aspect	0.360	0.932	0.08	<0.001
Substratum	0.617	0.786	0.11	<0.001

FIGURES:

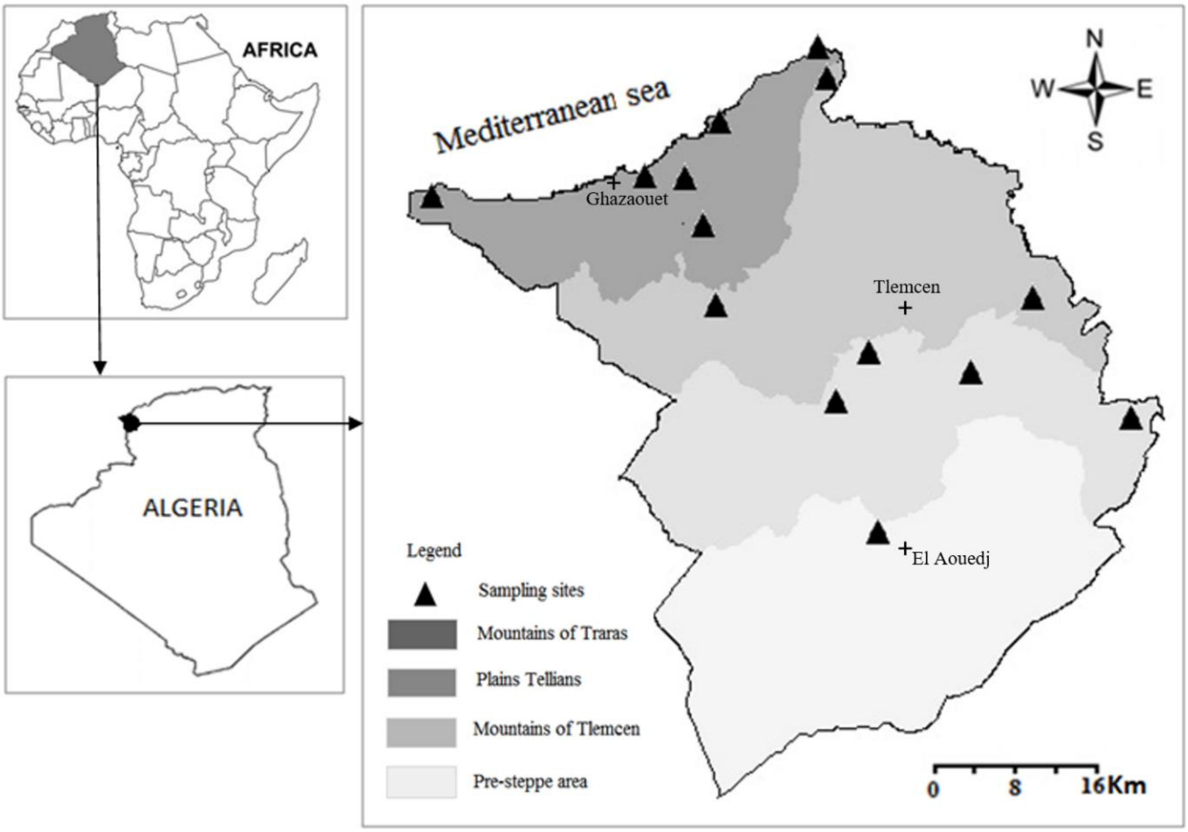

Fig 1. Localisation of the different sampling sites and major place names in the study area (Wilaya of Tlemcen, North West Algeria).

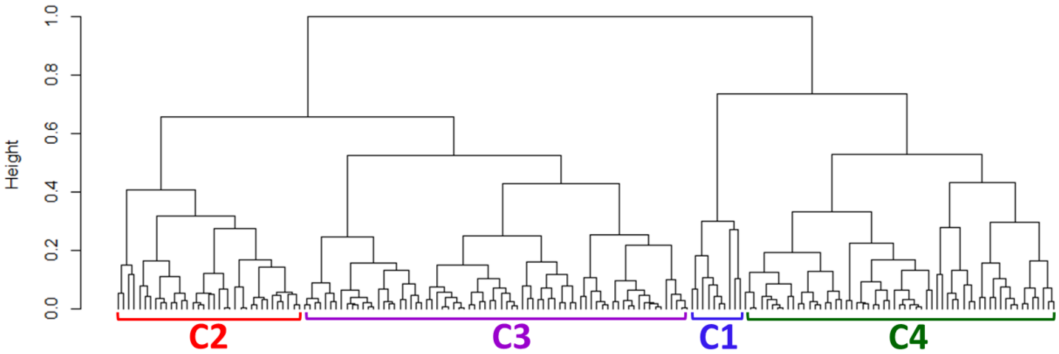

Fig 2. Community type classification derived after cluster analysis on the sample-plots scores of the first two DCA axes. Four main community types are depicted for the 177 study sites in North West Algeria.

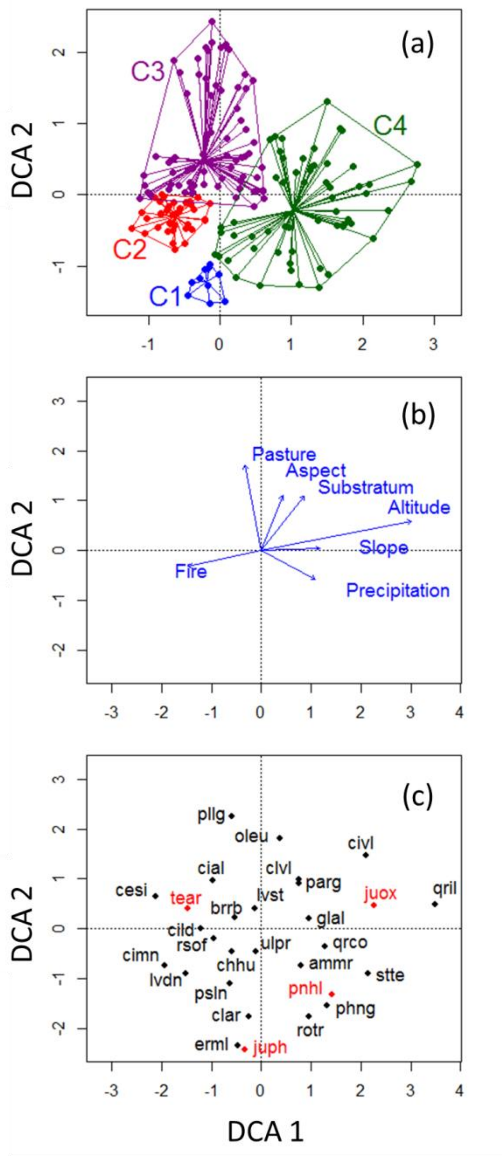

Fig 3. DCA ordination plots showing: (a) the position of the 177 sampling plots within the described community types. Each community is defined by the convex hull formed by sites composing them and their corresponding centroid. (b) Environmental variables fitted passively to the two first DCA axes. Longer vector lines represent stronger correlations. (c) Most frequent species found in the study area. Species code: ammr= *Ampelodesmus mauritanica*, brrb= *Bromus rubens*, cial= *Cistus albidus*, cesi= *Ceratonia siliqua*, cild= *Cistus ladaniferus*, civl= *Cistus villosus*, clvl= *Calicotome villosa*, chhu= *Chamaerops humilis*, cimn= *Cistus monspeliensis*, clar= *Cladanthus arabicus*, erml= *Erica multiflora*, glal= *Globularia alypum*, juox= *Juniperus oxycedrus*, juph= *Juniperus phoenicea*, lvst= *Lavandula stoechas*, lvdn= *Lavandula dentata*, oleu= *Olea europaea*, parg= *Paronychia argentea*, pllg= *Plantago lagopus*, pnhl= *Pinus halepensis*, phng= *Phillyrea angustifolia*, psln=

Pistacia lentiscus, qril= *Quercus ilex,* qrco= *Quercus coccifera*, rotr= *Rosmarinus tournefortii*, rsof= *Rosmarinus officinalis,* stte= *Stipa tenacissima,* tear= *Tetraclinis articulate*, ulpr= *Ulex parviflorus*.

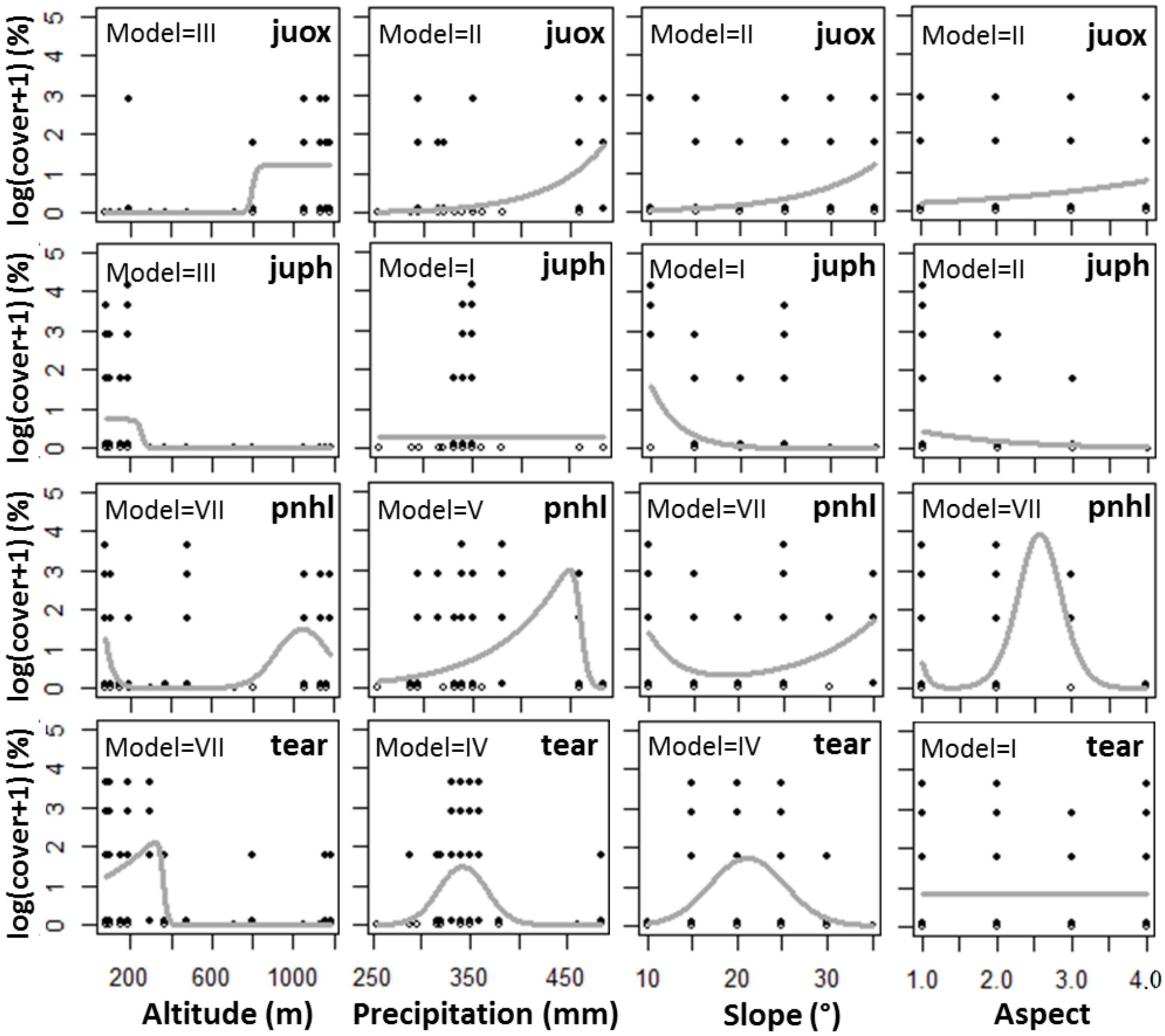

Fig 4. Huisman-Olf-Fresco **(**HOF) models for the four dominant coniferous species in relation to the most relevant environmental variables. juox = *J. oxycedrus*, juph = *J. phoenicea*, pnhl = *P. halepensis* and tear = *T. articulata*. Aspect shows an increasing gradient of aridity (1: north, 2: east, 3: west, 4: south).

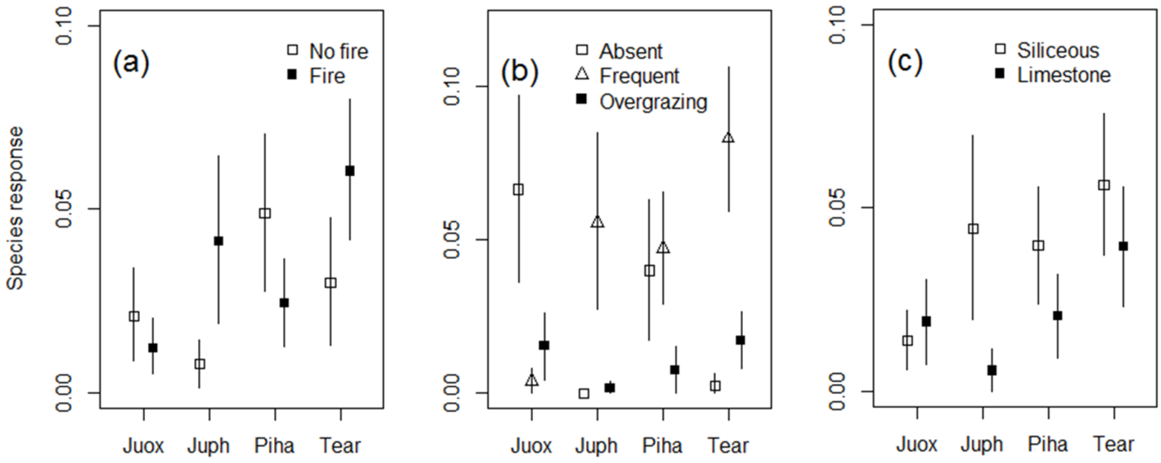

Fig 5. Species response to (a) fire and (b) grazing pressure and (c) substratum. Error lines indicate the 95% confidence interval assessed by bootstrapping.

Supplementary material

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