

LETTER

Priority conservation areas for *Cedrus atlantica* in the Atlas Mountains, Morocco

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Abstract

Assessing biodiversity loss and species extinction is necessary to warn society and raise awareness of the impacts of ongoing climate change. Prioritizing protected areas is the pragmatic and applicable management measure under the pressure of ongoing climate change and limited resources to conserve species at risk of extinction. We developed a novel conservation index (CI) to prioritize areas and populations of an endangered mountain tree species that need protection in the face of ongoing climate change, as conservation of all populations may not be realistic. This CI integrates (1) mountain topography to identify potential refugial areas with suitable microclimates, (2) genetic diversity to assess the adaptive capacity of local populations, and (3) hypothetical climate change in the species' range. We applied this CI to Atlas cedar, an endemic and threatened species whose populations are scattered throughout the Moroccan mountains. This index provided a scale for 33 populations studied and suggests that genetically diverse populations located in rugged areas where future local climate may overlap with their current climatic niche should receive a higher conservation priority. This index may also be applicable to other mountain species with scattered populations and is likely to be more accurate if more precise climate data are used at the microrefugia scale.

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KEYWORDS

Cedrus atlantica, climate-change, conservation index, genetic diversity, microrefugia, mountain ruggedness, protected areas

INTRODUCTION

Human-induced warming, which is proceeding faster in the highlands than in the lowlands, threatens mountain forests regardless of latitude (Albrich et al., 2020; Pepin et al., 2015). As a result, local extinction risk, especially of tree species, is expected to increase in the coming decades (Thomas et al., 2004), necessitating effective conservation measures. The identification of future suitable habitats and niches for mountain tree species is mostly based on model simulations (Burrows et al., 2014; Guisan & Thuiller, 2005). However, the complex topography of mountains introduces uncertainties in the climate data underlying all models (Thakur et al., 2021), making the de facto conservation of forest species in mountain regions a challenge (Albrich et al., 2020).

Given the continuing threats to forest ecosystems in mountain regions and the need for effective conservation measures, extensive knowledge from field observations including fossil records, quantitative ecology, geoscience, and population genetics appears necessary (Sutherland et al., 2009). Furthermore, these conservation efforts should be planned for the long term, taking into account species resilience, migration rates, and the ability to recolonize new habitats over time (Gillson & Marchant, 2014). Fossil records have shown that during the last ice age, mountain species survived in very limited areas known as “refugia” when the climate was unfavorable. Refugia can be defined as mountainous habitats that can support small or reduced populations of several species during a period when the global climate is unfavorable for a larger geographic area (Bennett & Provan, 2008). Based on the concept of glacial refugia, ecoevolutionary studies suggest that isolated populations may survive in so-called “future microrefugia” where local climate may diverge from global climate, as it did in the past (Keppel et al., 2018). For many tree species in mountainous regions, microrefugia may be the only alternative to extinction, especially if their migration rate is lower than the rate of climate change (Ashcroft, 2010; Hannah et al., 2014). Microrefugia are particularly promising in mountainous regions because they may have precipitation/humidity and temperature conditions that are more suitable for plant species than the prevailing regional climate (Dobrowski, 2011; Keppel et al., 2012; Rull, 2009). An effective conservation plan should incorporate a network of microrefugia that can support seed dispersal and species migration and thus gene flow between populations (Hannah et al., 2014).

In North Africa, the Atlas Mountains provided a particularly rich diversity of microclimates for plant species, enabling them to compensate for unfavorable global climate variability over geological time (Hughes et al., 2011). In addition, tree species of Mediterranean forests are resilient to disturbance (Lavorel, 1999) and resistant to drought, which has allowed them to persist locally over geological time. However, the continued and rapid decline in annual rainfall (Schröter et al., 2005; Walther et al., 2002) with recurrent extreme droughts in recent decades in North Africa (Esper et al., 2007; Ladjal et al., 2005; Linares et al., 2011) will shorten the recovery time of the species and put them at risk (Gazol et al., 2018). Among the threatened species in North Africa today is the endemic Atlas cedar (*Cedrus atlantica* [Endl.] Manetti ex Carrière) (Thomas, 2013), whose range shrank dramatically and whose lower elevation shifted upwards by more than 100 m (Cheddadi et al., 2017; Rhanem, 2011). In 2016, the Atlas cedar was included in the World Network of Biosphere Reserves (en.unesco.org/biosphere/arab-states/atlas-cedar) and the mountains in Morocco are now considered critical habitat for conservation by the United Nations Educational, Scientific and Cultural Organization. In this context, the Moroccan Ministry of Forestry has designated several national parks and biosphere reserves to protect biodiversity and species including the Atlas cedar (www.eauxetforets.gov.ma/Biodiversite/GestionBiodiversite). These initiatives are necessary and have helped to preserve biodiversity in Morocco. However, preserving all populations of a species may not be realistic. In addition, protected areas that are suitable today may prove unsuitable in the future (Lawler et al., 2020). An approach based on an assessment of the suitability of the areas to be protected and the adaptive capacity of local populations will be much more effective in the long term. Previous studies based on species mapping (Belote et al., 2017), botanical surveys (Bou Dagher-Kharrat et al., 2018), protected area networks (Lawler et al., 2020), and genetic diversity (Mattera et al., 2020) have shown that prioritizing protected areas for species conservation should maximize the efficiency of conservation efforts.

In the present study, we developed a novel conservation index (CI) based on mountain topography, climate, and population's genetics to identify potential future suitable conservation areas and *ad hoc* populations to efficiently conserve the Atlas cedar in the long term. Such an index will provide conservation planners with

integrated scientific data on which populations of an endangered species should receive higher conservation priority because they may have the greatest potential to cope with ongoing climate change.

MATERIAL AND METHODS

Our approach to identifying and prioritizing protected areas for Atlas cedar is based on a strategy that considers the ability of a suite of populations to survive locally and the effective cost of their protection over the long term. To develop such a strategy, we assess both the suitability of the habitat and the adaptive capacity of the populations that make up the species' range in the face of ongoing climate change. Because not all populations that make up the species' range are located in suitable future habitat or may lack the capacity to adapt locally, we developed a CI that considers (1) a climate that may differ from the current one, (2) the suitability of the area where the species occurs as future habitat for local populations, and (3) the potential genetic capacity of populations to adapt locally to climate change in the long term.

Past and present Atlas cedar range

Changes in the range of a species in the past provide information about its ability to survive in isolation and to

colonize new areas under different past climatic conditions. The biogeographic changes of Atlas cedar in the past can be reconstructed from fossil pollen. We compiled a dataset of 13 fossil pollen records from the Rif, Middle Atlas, and High Atlas Mountains from published and new data (Table 1). The fossil records are distributed over a wide altitudinal range from sea level to over 2600 m asl. Seven records are located within the modern Atlas cedar range (Ifrah, Hachlaf, Ras El Ma, Tifounassine, Sidi Ali, Tigalmamine Ait Ichou), two at the upper and lower edges of the mountains (Tislit and Aanasser, respectively) and four outside the modern range (Mhad; Bab El Karn; Oudadane and Inouzane). In terms of time span, each fossil pollen record covers a different period within the last 25,000 years (Table 1). The records in the Rif Mountains cover part of the Holocene (11.7 ka to present), while the records in the Middle and High Atlas cover the postglacial period or go back to the last glacial maximum (21 ka). The pollen records from Hachlaf and Tifounassine in the Middle Atlas are new and previously unpublished.

The current range of Atlas cedar was determined based on coarse maps (M'Hirit, 1999), corrected and supplemented with georeferenced populations by the first author during several field trips between 1996 and 2018. Atlas cedar forests occur in the Rif, Middle Atlas and High Atlas between about 1400 and 2300 m asl with an area of 17,200, 86,000, and 26,800 ha, respectively (official range estimate of the "Service des Etudes et de l'Inventaire Forestier National"). Using this modern

TABLE 1 Table showing the geographical location of 13 fossil pollen records from the Rif (light green), Middle (green), and High Atlas (dark green)

	Label	Site name	Longitude	Latitude (°N)	Altitude (m. asl)	Time span (ka)	Authors
Rif	MH	Mhad	-5.438668	35.128395	754	0-6	Cheddadi et al. (2017)
	BK	Bab El Karn	-5.206978	35.022524	1178	0-9	Cheddadi et al. (2017)
	AA	Aanasser	-4.992503	35.017629	1342	0-3.5	Cheddadi et al. (2017)
	OU	Oudadane	-3.254175	35.215023	10	6-11	Zapata et al. (2013)
Middle Atlas	IF	Ifrah	-4.934143	33.556393	1620	8-25	Cheddadi et al. (2009)
	HA	Hachlaf	-4.999410	33.550543	1700	0-16	Tabel (2015)
	RM	Ras El Ma	-5.223611	33.58306	1633	0-18	Nour El Bait et al. (2014)
	TF	Tifounassine	-5.095831	33.152704	1921	0-15	Tabel (2015)
	SA	Sidi Ali	-5.010007	33.063093	2080	0-8	Lamb et al. (1999)
	TG	Tigalmamine	-5.343285	32.905075	1626	0-12	Lamb et al. (1995)
	AI	Ait Ichou	-5.565	32.6875	1661	0-17	Tabel et al. (2016)
High Atlas	TS	Tislit	-5.634758	32.197266	2260	0-19	Cheddadi et al. (2021)
	IN	Inouzane	-5.455367	32.208381	264	0-6	Reille (1976)

Abbreviations: AA, Aanasser; AI, Ait Ichou; BK, Bab El Karn; HA, Hachlaf; IF, Ifrah; IN, Inouzane; MH, Mhad; OU, Oudadane; RM, Ras El Ma; SA, Sidi Ali; TF, Tifounassine; TG, Tigalmamine; TS, Tislit.

georeferenced range of Atlas cedar, we assessed its climatic niche. The niche of a species can be defined by *in situ* variables or resources or *ex situ* variables or conditions, which are environmental variables such as temperature and precipitation (Soberón, 2007). The greatest threat to modern populations of Atlas cedar is ongoing climate change, which is dramatically affecting the species' climatic niche and threatening it with extinction (Thomas, 2013). Therefore, we focused on the species' current climatic niche and its future evolution. To estimate the modern niche, we used monthly precipitation and temperature values from the CHELSA climate dataset (Karger et al., 2017, <https://chelsa-climate.org>), which we interpolated to georeferenced Atlas cedar populations. Atlas cedar is a Mediterranean species whose climatic niche is characterized by contrasting seasonal precipitation and temperature (Figure 2).

The species inhabits areas with seasonal average precipitation ranging from 25 mm in summer to up to 275 mm in winter and an average temperature of 5°C in winter and 20°C in summer (Figure 2). However, Atlas cedar tolerates snowy winters with minimum temperatures in the coldest month down to -8°C (Ducrey, 1981), suggesting that the

species may occupy a broader range than its current one. Atlas cedar is relatively tolerant of different soil types (M'Hirit, 1999) and a climate with marked seasonal variations in precipitation and temperature.

Terrain analysis

Mountain topography is an important variable in providing local suitable habitat for terrestrial species (Steinbauer et al., 2018; Whittaker et al., 1973). A quantitative measure of topography change using a ruggedness index or topographic position index may be important in predicting suitable habitat for species (Kübler et al., 2015). In this study, we use the Terrain Ruggedness Index (TRI) derived from digital elevation models. TRI is the difference in elevation between a grid cell and its eight neighboring cells (Riley et al., 1999). We used GIS (QGIS Development Team, 2019) to calculate the TRI (Figure 3) using a GTOPO30 digital elevation model (USGS EROS Archive, n.d) with a spatial resolution of 30 arcseconds (~ 1 km). Riley et al. (1999) classified the TRI with values and thresholds ranging from 0 (flat) to over 1000 (extremely rugged).

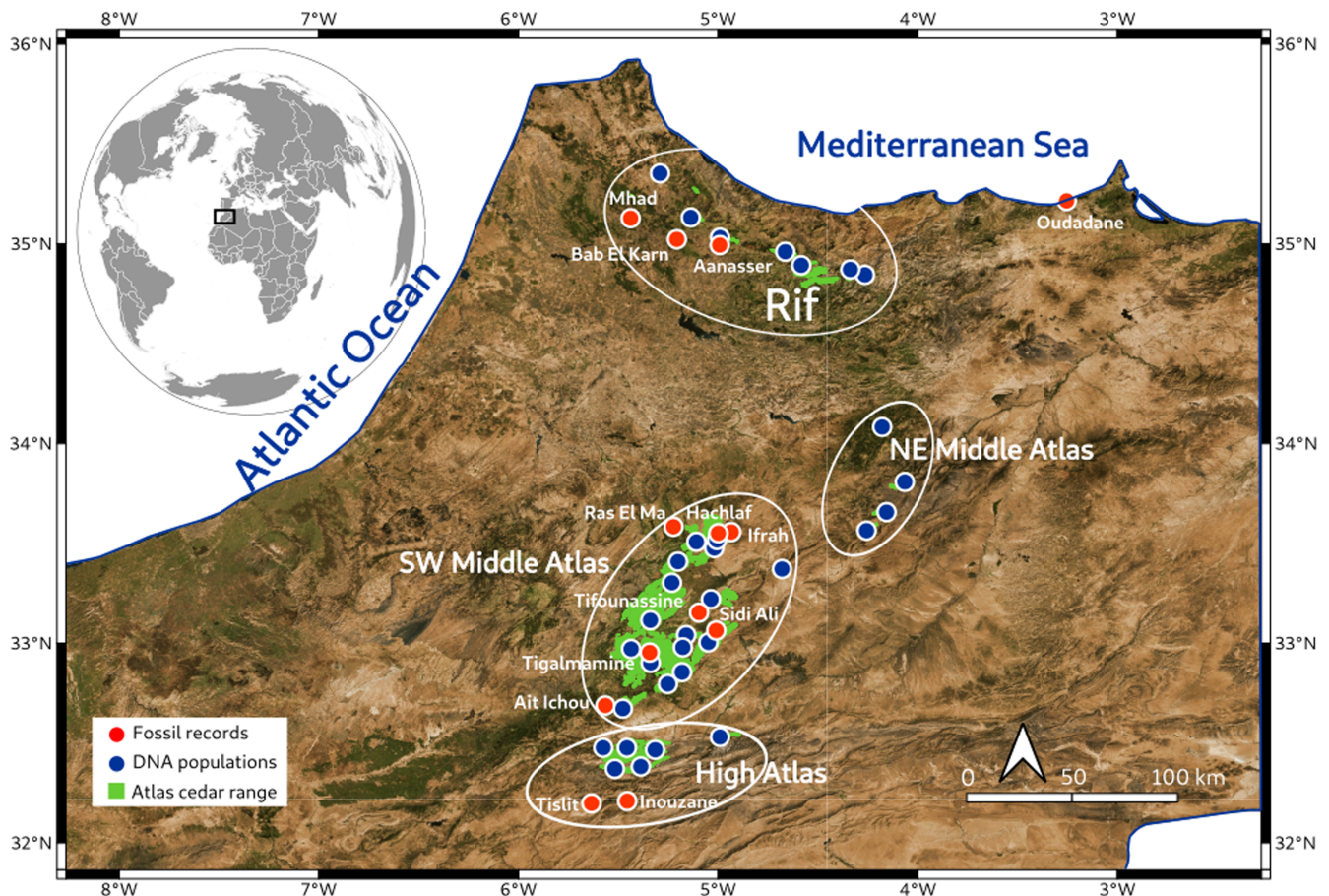


FIGURE 1 Location of fossil records (red circles) and populations sampled for the genetic study (blue circles) over the Atlas cedar range (green)

Estimation of the genetic diversity

In general, trees often have high genetic diversity, high outcrossing rates, and high plasticity (Petit & Hampe, 2006), which gives them great adaptability to climate (Christmas et al., 2016; Davis & Shaw, 2001). Various measures of genetic diversity (allelic richness, expected heterozygosity) have been considered for conservation plans. In this study, as suggested by Petit et al. (1998) for the argan tree in Morocco, we considered allelic richness as an appropriate measure of genetic diversity for Atlas cedar.

We sampled 33 populations of Atlas cedar in October 2017, including seven populations in the Rif, 20 in Middle Atlas and six in the High Atlas (Figure 1). We collected samples from five individuals per population targeting old trees, with at least 100 m between two sampled trees. Needles were preserved dried in silica gel before DNA extraction using the DNeasy 96 plant kit (QIAGEN GmbH).

Allelic richness (Figure 3) was estimated by microsatellite polymorphism analysis. Microsatellite data were generated according to De Barba et al. (2017). This allowed the design of 15 new highly polymorphic microsatellites that can be amplified in a single PCR multiplex (Table 2). Two replicate multiplex PCRs were performed for each sample to reduce potential genotyping errors. Reactions were performed in a volume of 25 μ l and contained 1x concentrated Platinum Multiplex PCR Master Mix (Applied Biosystems™), 0.1 μ M of each of the 30 primers and 2 μ l of DNA extract. The thermocycling

profile had an initial denaturation step of 2 min at 95°C, followed by 40 cycles of 30 s at 95°C, 90 s at 50°C, 60 s at 72°C, and a final elongation step of 10 min at 72°C. PCR products were purified using the MinElute PCR Purification Kit (QIAGEN GmbH). PCR products were then sequenced on a HiSeq 2500 (Illumina) using a paired-end strategy (2 \times 125 bp). Genotypes were generated for each sample and for each microsatellite. Genotypes were only included if the results of the two PCR replicates were identical. If the two replicates were not identical due to allelic dropout or the presence of a false allele (Taberlet et al., 1996), the corresponding genotypes were recorded as missing data. Missing data were rare (1.17% of the total data set). Mean allelic richness across all loci was calculated in genetix (Belkhir, 2004).

Conservation index

The CI integrates species genetic diversity, mountain ruggedness and hypothetical change in temperature and precipitation (Figure 2 and Table 3). The CI is constructed as follows:

$$CI = Gd * Tr / \max(Di),$$

where Gd is a measure of genetic diversity, Tr is the highest terrain ruggedness where populations occur today, and Di is the Euclidean distance between the future temperature and precipitation at the population

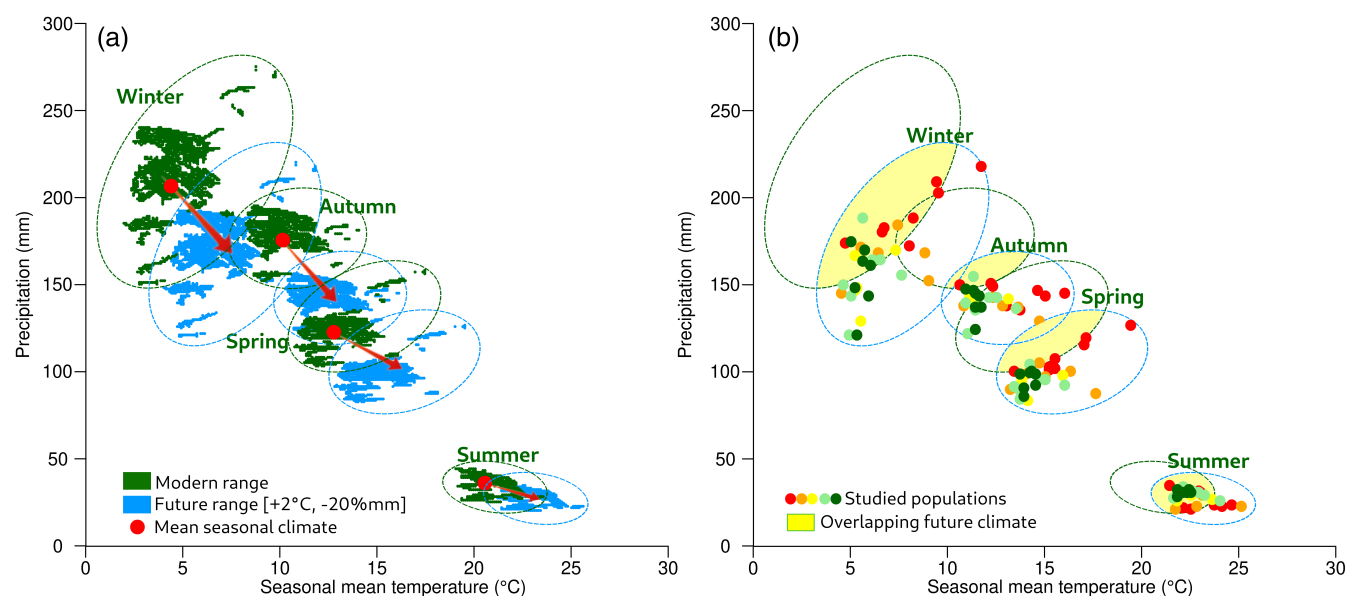


FIGURE 2 (a) Modern seasonal climate of the Atlas Cedar in Morocco (green area) with a hypothetical climate scenario with a 2°C increase in average temperature and 20% less precipitation (blue area). Red arrows illustrate these seasonal shifts. Dashed lines delineate present (green) and an expected future (blue) seasonal climate. (b) Seasonal climate at the sites of the 33 populations studied (colored dots). Colors correspond to the quantiles of the conservation index (see Table 3). The yellow areas represent the overlap between modern and future climate (as in [a])

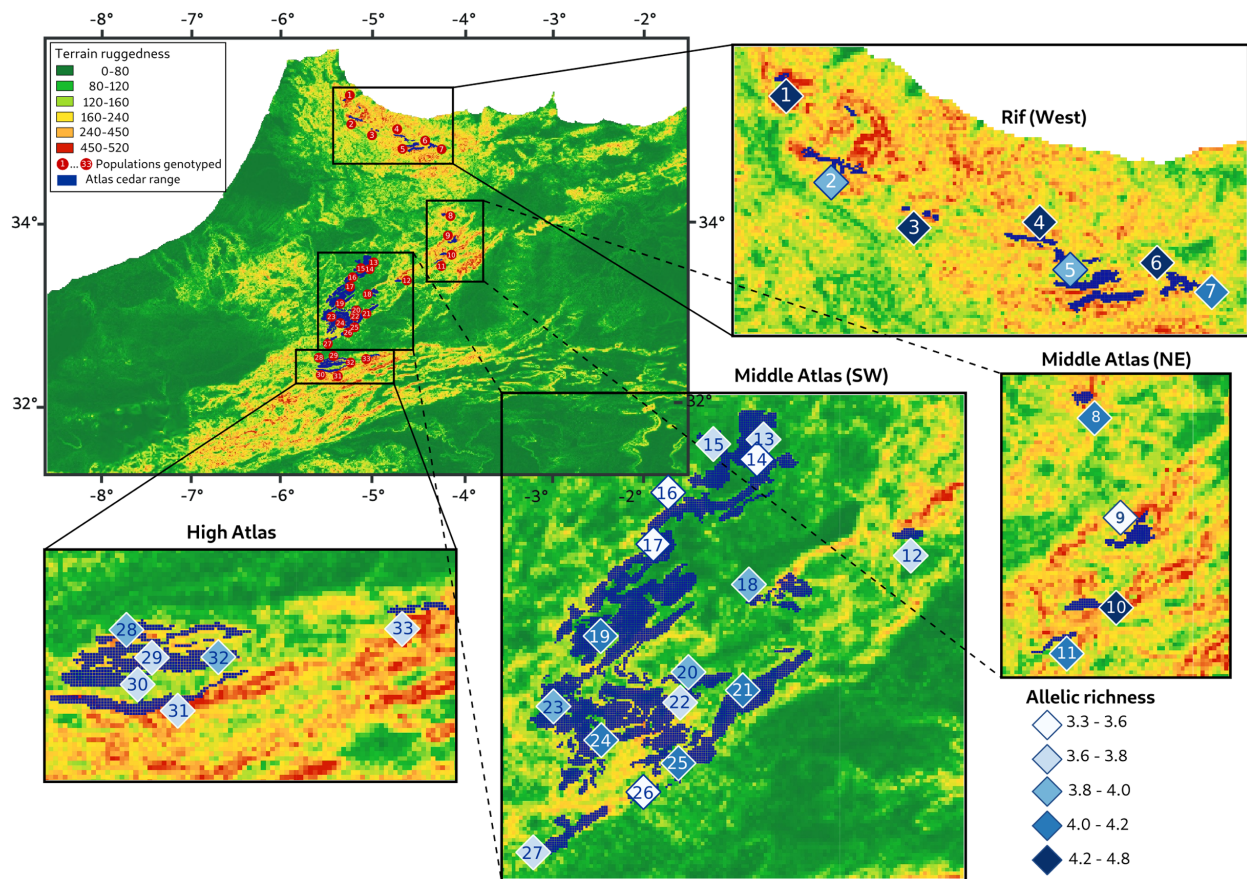


FIGURE 3 Terrain Ruggedness Index map of northern Morocco showing the range of Atlas cedar (dark blue) and the allelic richness of populations sampled for the genetic study (blue graded diamonds with population numbers). The upscaled maps for the western Rif Mountains, the NE and SW Middle Atlas, and the central High Atlas show allelic richness in a more detailed landscape

TABLE 2 Primer sequences of 15 microsatellites of *Cedrus atlantica* used to estimate allele richness

Code	Forward primer (5'-3')	Reverse primer (5'-3')	Length (bp)	Nb alleles
ced02	ATGGATAGATAAATAGATGGAT	CTTGTGCCACACCATAG	48–80	11
ced03	CATAAATAATGATGATGTGTG	ATGTATTGTTTCTATTTTAGG	26–62	11
ced04	TTTTGGTGTTTGAATAGCTC	GGGAAAGGGTAGGTATG	30–54	13
ced09	CAACCCTAGATCTCCA	TGGTTGGCTACAGCTGA	30–54	7
ced14	AAGAATAAGTTAAATAAGAGTGT	GGCTCTTCATTTAGTGTGA	29–61	13
ced17	CGATTAATATATAAATAACACAC	ACTTTATTTATTTTCTTAGTGA	46–94	34
ced18	AGTACATACATCCATGCATA	TTGAGGTGCCCAAGCAA	38–81	9
ced23	GTAGATGGATTAGATAGGTA	CTATCTACCTAGCTATATAC	33–97	12
ced24	TGAGCTAAAAGTTTGGGCT	TCTATGTAGCCATCTTGGA	34–62	7
ced28	AGTATTTTAATCCTATCTTTTCG	CCTGTACTAATAGGTATAAG	35–91	21
ced36	ATTGGGTTGACAACCTTACT	TTGATTTTCAATTTGTTAAGTG	21–69	17
ced43	GCTTCATGGTCATAAACTC	GTGTCCTCAATACTCTCAT	20–76	12
ced49	TTTCTGCTCCAACAACAT	CTTATGAGAAAATGTTTCTTG	49–85	24
ced51	GAAGAAATCAGATTATAGATAG	GTTTGTGATTTTGATGCATG	30–66	10
ced56	GTTTGTAGAAATTTGAAACCA	TTAGTAGTTTGTATTGTCATAC	31–79	16

Note: The number of alleles found in the 183 individuals analyzed and the length variation (without primers) are indicated. Since genotyping was based on sequence data, multiple alleles show sequence variation at the same length.

location and the mean of the species' modern temperature and precipitation for each season (i = winter, spring, summer, and fall). In the case of this study, we assumed a hypothetical future climate where temperature and precipitation are 2°C warmer and 20% lower than today, respectively (Figure 2). This future climate scenario is a simple and hypothetical climatic shift of the modern climate over the Moroccan Atlas Mountains, but it is consistent with model simulations (Gao et al., 2006).

For Gd, we used allelic richness as a measure of genetic diversity, which is considered an important genetic marker for conservation purposes (Petit et al., 1998), but other genetic markers can also be considered. Regarding climate change, we used mean seasonal temperature and precipitation. However, if other climate variables are more important for the threatened species or other climate scenarios are available, these can also be considered.

TABLE 3 Conservation index (CI) based on genetic diversity (Gd), terrain ruggedness (Tr), and distance (Di) between present climate and a future expected climate in which temperature will increase by +2°C and precipitation will decrease by 20%

Pop	Area	Site name	Longitude	Latitude	Gd	Tr	Di	CI
1	Rif	Jbel Kelti	-5.29711	35.357585	4.2667	522	31	71.85
2	Rif	Talassemtane	-5.137349	35.132118	4	480	29	66.21
19	SW MA	Ouiouane	-5.33959	33.11428	4.1333	372	26	59.14
3	Rif	Tiziren	-4.99113	35.031065	4.4	360	32	49.50
18	SW MA	Timahdit	-5.036378	33.219811	3.9333	401	32	49.29
16	SW MA	Ain kahla	-5.20134	33.40802	3.6	319	25	45.94
6	Rif	Oursane	-4.337971	34.871228	4.8	313	37	40.61
4	Rif	Bab al arz	-4.663953	34.960423	4.3333	362	40	39.22
8	NE MA	Tazzeka	-4.178251	34.082275	4.0667	520	54	39.16
5	Rif	Issaguen	-4.583744	34.892497	3.9333	362	37	38.48
31	HA	Assaka	-5.387568	32.38148	3.8	610	61	38.00
24	SW MA	Tigalmamine	-5.33833	32.90126	4.2	322	38	35.59
7	Rif	Sidi Boutmim	-4.264684	34.844568	4.0667	312	38	33.39
22	SW MA	Col du zad	-5.17686	32.97816	3.7333	270	35	28.80
9	NE MA	Maghraoua	-4.065139	33.807234	3.6	587	77	27.44
28	HA	Tikajouine	-5.457128	32.47518	3.9333	391	58	26.52
30	HA	Bouadil	-5.447436	32.416967	3.6667	410	60	25.06
21	SW MA	Sidi ali	-5.04891	33.00329	4.0667	245	40	24.91
23	SW MA	Azigza	-5.43617	32.97037	4	224	36	24.89
33	HA	Taouraoute	-4.991155	32.529588	3.8	388	63	23.40
17	SW MA	Afenourir	-5.23176	33.30239	3.3333	146	21	23.17
25	SW MA	Tanwourdi	-5.1805	32.85409	4.0667	237	42	22.95
27	SW MA	Ait Ichou	-5.4775	32.67166	3.6667	297	51	21.35
32	HA	Tounfite	-5.315822	32.465321	3.9333	292	56	20.51
26	SW MA	Tizi nghachou	-5.252179	32.795194	3.5333	233	42	19.60
10	NE MA	Taffert	-4.156541	33.65593	4.4	378	85	19.57
20	SW MA	Bakrit	-5.16006	33.04051	3.8667	159	32	19.21
12	SW MA	Tichoukt	-4.680126	33.371152	3.6667	325	63	18.92
15	SW MA	Ifrane NP	-5.10916	33.50719	3.6667	175	36	17.82
29	HA	Sidi yahia	-5.433238	32.464374	3.7333	276	58	17.77
11	NE MA	Timghilt	-4.256628	33.563334	4.2	343	85	16.95
13	SW MA	Hachlaf	-5.00636	33.51648	3.8	150	45	12.67
14	SW MA	Ifrane NP	-5.019888	33.475924	3.4	146	43	11.54

Note: The colors correspond to the quantiles of the conservation index.

Locations of genotyped populations of Atlas cedar (Figure 1) differ from raster-based terrain data (USGS EROS Archive, Figure 3) and climate data (Karger et al., 2017). Therefore, we considered the highest terrain ruggedness and mean climate data for the areas where the studied populations occur for the CI.

This ecoevolutionary CI has no equivalent in known conservation approaches (Gavin et al., 2015; Lindenmayer et al., 2006; Schemske et al., 1994). It represents a novel tool that can be adapted and applied to other fragmented and threatened species under different climate scenarios.

RESULTS

Past and present biogeography of the Atlas cedar

In the Middle Atlas, there are small amounts of pollen grains of Atlas cedar in several sites over the time span

between 20 and 10 ka (Figures 4 and 5). In the High Atlas, there is only one pollen record from Lake Tislit, where no pollen grains of Atlas cedar are found during this time period. Lake Tislit is located at high altitude (2200 m asl) where an ice sheet was present during the last glacial period until the beginning of the Holocene (Cheddadi et al., 2021; Hughes et al., 2018). In the Rif Mountains, pollen records cover only the Holocene period, but they are at lower elevations than those in the Middle and High Atlas, allowing us to extend our observation of past dynamics of Atlas cedar populations to a wider spatial range.

During the Holocene, we observed pollen occurrences of Atlas cedar in all mountains from sea level in the northern part of the Rif to about 2600 in the High Atlas (Figures 4 and 5). However, there are differences in pollen proportions at different altitudes, reflecting changes in population density around the sites. The pollen record from Oudadane is from an archeological site located at sea level (Figure 1). It shows that the proportion of pollen

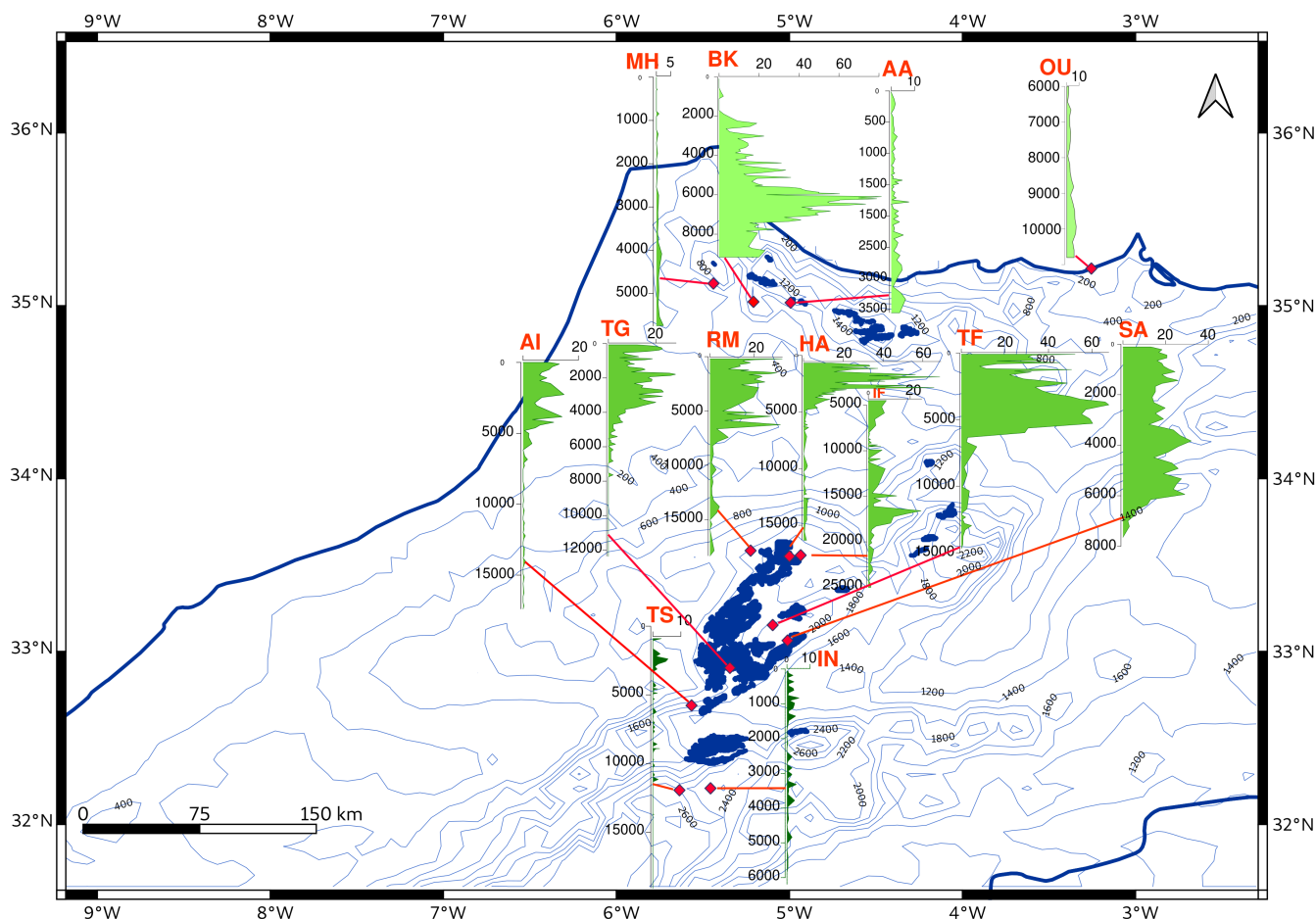


FIGURE 4 Map showing the percentage of Atlas cedar pollen in 13 fossil records from the Rif Mountains (light green; Mhad [MH], Bab El Karn [BK], Aanasser [AA] and Oudadane [OU]), the Middle Atlas (green; Ifrah [IF], Hachlaf [HA], Ras El Ma [RM], Tifounassine [TF], Sidi Ali [SA], Tigalmamine [TG] and Ait Ichou [AI]), and the High Atlas (dark green; Tislit [TS] and Inouzane [IN]) over its modern range (blue area). The Y axis shows the age of pollen records in calendar years BP

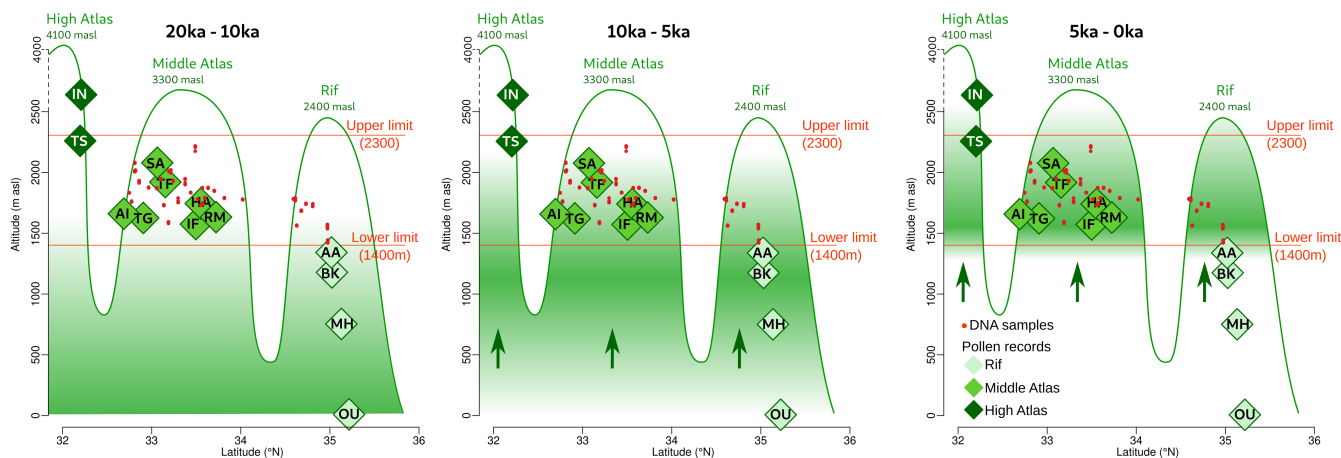


FIGURE 5 Three time span diagrams showing the potential altitudinal distribution (green shaded area) of Atlas cedar in Morocco and its potential migration between 20 ka and today (0 ka) based on the 13 fossil pollen records from the Rif (Mhad [MH], Bab El Karn [BK], Aanasser [AA] and Oudadane [OU]), the Middle Atlas (Ifrah [IF], Hachlaf [HA], Ras El Ma [RM], Tifounassine [TF], Sidi Ali [SA], Tigalmamine [TG] and Ait Ichou [AI]), and the High Atlas (Tislit [TS] and Inouzane [IN]). The horizontal red lines indicate the present-day upper and lower limits of atlas cedar in Morocco

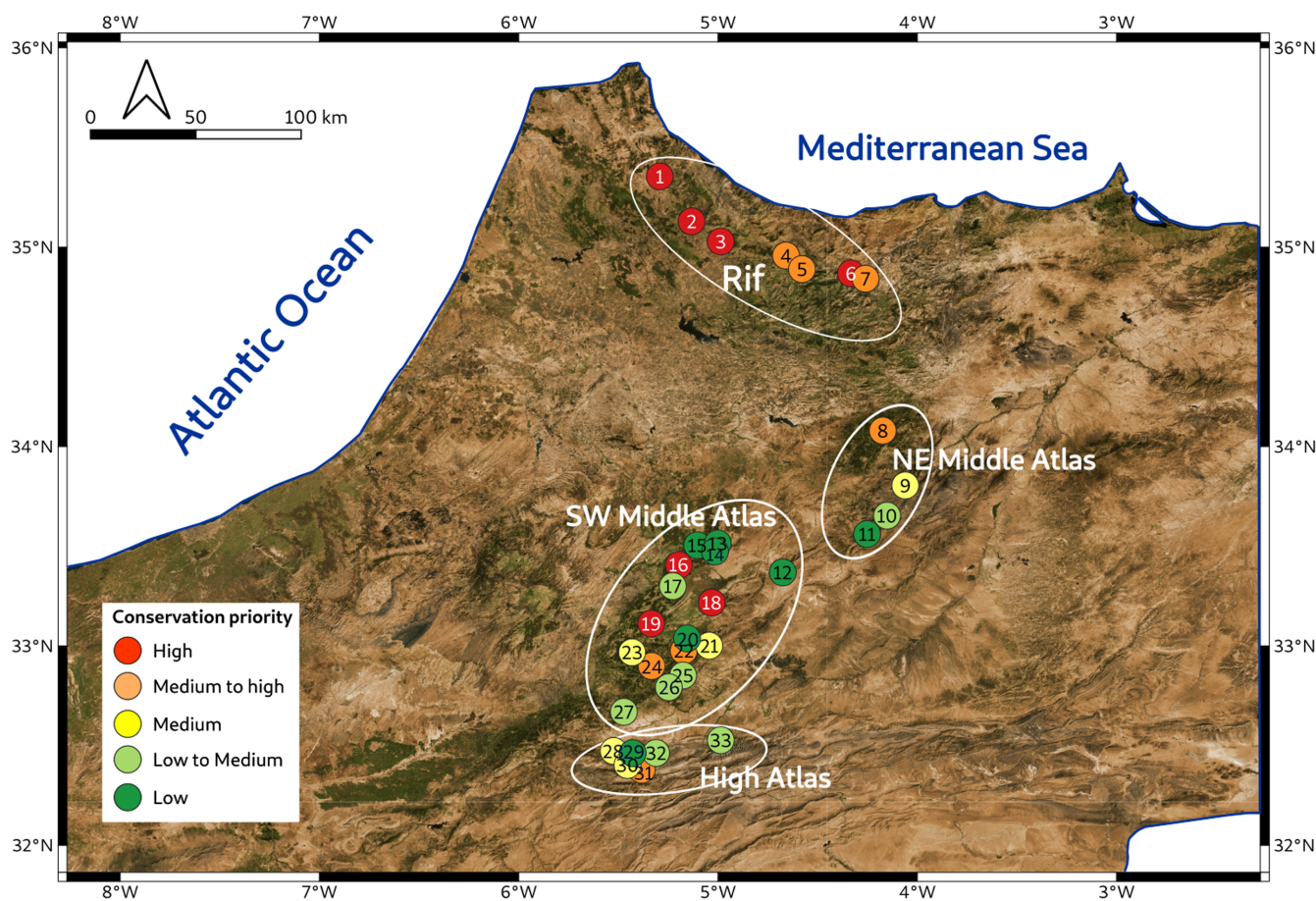


FIGURE 6 Conservation index map showing recommended priorities for Atlas cedar populations from low (green) to high (red) priority

grains of Atlas cedar was greater than 2% between about 11 and 6 ka (Figure 4). Atlas cedar pollen grains are less than 1 km from their trees of origin (Wright, 1952), and

their continuous occurrence in the Oudadane record indicates the proximity of the species to sea level during the early Holocene. After 6 ka, we observe a marked

decline in the Rif pollen records with extinction at altitudes below 1200 m asl. In the Middle Atlas, the species occurs at all sites higher than 1600 m asl (Figure 5). After 4 ka we observe a steady decline in pollen occurrence, but unlike in the Rif Mountains, the Atlas cedar is not yet extinct after 2 ka. In the High Atlas, the species is absent during the last ice age and does not spread during the Holocene, but some populations may have reached elevations higher than the present upper limit (Figure 4).

The present small and isolated populations of Atlas cedar are located in the Rif, NE of the Middle Atlas and in the central part of the High Atlas, where the mountain topography is more rugged than in the SW of the Middle Atlas, where the more extensive populations are located today (Figure 3).

Index for decision making in conservation

We classified the 33 populations of Atlas cedar studied into five equal groups using CI quantiles to rank their conservation priority between high and low (Table 3 and Figure 6). The populations that should be given the highest conservation priority are the most genetically diverse, are located in rugged areas, and the hypothetical future climate still overlaps with or comes very close to their current locations (Figure 2), bearing in mind that the current climatic niche is clearly constrained by human activities (Cheddadi et al., 2015). Populations with the highest conservation priority are located in the Rif, at NE in the Middle Atlas and the central part of the Middle Atlas, and one population in the High Atlas (Figure 6). These populations constitute a network in the Moroccan mountains that should be protected for the conservation of genetic resources. Populations in the NE of the Middle Atlas with lower CI have high genetic diversity (in Taffert and Timghilt), but they are located in areas that are not highly rugged (Table 3) and therefore may not provide future suitable climatic refugia. Several populations in the SW of the Middle Atlas have low genetic diversity and are located in less rugged landscapes that may expose them more to the ongoing climate change.

DISCUSSION

Himalayan *Cedrus deodara* is the common ancestor of the three Mediterranean species, *C. atlantica*, *C. libani* and *C. brevifolia* (Panetsos et al., 1992). The genetic split of *C. atlantica* from the two Eastern Mediterranean species and its immigration to North Africa occurred in the Tertiary at about 25 Ma (Qiao et al., 2007). The oldest observed occurrences of *Cedrus* in northern Morocco are

from a fossil pollen record dating to the Messinian (ca. 7.2 to ca. 5.3 Ma) (Feddi et al., 2011). Recent fossil pollen data suggest that *Cedrus* was present in northern Morocco during the last two climatic cycles (ca. 250,000-years) (Ramos et al., 2008). Our fossil pollen dataset (Figure 4) shows that the range of Atlas cedar has varied widely since the last ice age and throughout the Holocene, with extensive populations from sea level in the Mediterranean borderlands to mountainous areas above 2000 m in the High Atlas during the late Holocene (Figure 5). Today, Atlas cedar does not occur in any of the Moroccan mountains below about 1300 m asl and several populations are extinct in the Rif (Abel-Schaad et al., 2018; Cheddadi et al., 2017) and the Middle and High Atlas (Figures 3 and 4). The most extensive populations of Atlas cedar are now found at elevations above 1400 m in the central and southern parts of Middle Atlas, where they cover more than 125,000 hectares. Smaller and scattered populations are found in the Rif Mountains (16 k ha), on NE of the Middle Atlas (6 k ha) and in the High Atlas (25 k ha) in or near highly rugged areas (Figure 3). These areas should be considered as potential modern microrefugia, as they still provide suitable habitats for fragmented relict populations.

Atlas cedar adapted its range to the last ice age and to Holocene warming by moving up and down in elevation (Figure 5). These past elevational movements and the possible persistence of isolated populations in scattered refugia left an imprint on the overall genetic diversity of the species. The genetic survey we conducted over the range of Atlas cedar (Figure 3) shows that Atlas cedar has a limited spatial genetic structure (as previously observed (Cheddadi et al., 2009; Renau-Morata et al., 2005; Terrab et al., 2008). If anything, the fossil and genetic data suggest that Atlas cedar had the ability to cope with advert past climates over the last climatic cycles by locally adapting its range and surviving in micro-refugia.

Records from before the instrumental era (Jouzel et al., 2007) show a similar amplitude of climatic oscillations as the current climate and the expected climate in the next decades. However, the main difference between the past millennia and the next century is the timescale over which climate change will occur and impact ecosystems and species (Nolan et al., 2018). Will today's fragmented populations of Atlas cedar have the capacity to survive under ongoing climate change? The critical issues are that the velocity of ongoing climate warming (Loarie et al., 2009) is higher than past natural global warming and the impacts on mountain landscapes are more pronounced (Bertrand et al., 2011; Lenoir et al., 2008), which will likely prevent the Atlas cedar from migrating naturally to seek suitable habitat. A hypothetical climate change with a seasonal increase of temperature with 2°C

and a decrease of 20% in precipitation will make local climate unsuitable for about 70% of the current forests of Atlas cedar (Figure 2). If the species were to face the latter hypothetical scenario, one way to save it from extinction is to maintain the most suitable populations locally in microrefugia. As other scientists have also noted local protected areas are likely to play an increasingly important role for species conservation and need greater protection (Barrows et al., 2020; Elsen et al., 2020; Hannah et al., 2007; Lawler et al., 2020; Morelli et al., 2020). However, a local climate may not be suitable. Mountains may contain a wide range of microhabitats and microclimates for long-term survival of upland tree species (Morelli et al., 2020). The approach of maintaining populations of a plant species locally would be more successful if we assess its genetic diversity with modern molecular markers (Barrows et al., 2020; Pautasso, 2009), analyze the ability of the mountain to provide a microrefugium (El Hasnaoui et al., 2020; Valencia et al., 2016), use historical information to understand long-term dynamics and potential resilience (Birks, 2012), and consider the most influential climate factors such as expected increasing aridity in the Mediterranean (Gao et al., 2006).

The Atlas cedar is a threatened species (Thomas, 2013), but conservation of all populations that make up its range would likely be an unrealistic effort, and all populations are clearly not equivalent for a global conservation plan. Conservation management of the species would be more efficient in the long term if it is focused on both the most suitable areas and the potentially best adapted populations. Based on its environmental history and modern observations, including its genetic diversity, we constructed an index (CI) (Figure 6 and Table 3) to determine which populations should receive a more sustained conservation effort because they may represent a better option or more viable opportunity for the persistence of the Atlas cedar in North Africa. This CI allows the establishment of a priority scale for conservation efforts, as conservation of all populations in Morocco is not possible due to limited resources, even though the species is considered to be in danger of extinction.

All populations located in the Rif Mountains have higher allelic richness than those in the Middle and High Atlas. Moreover, they are also located within or near areas of high terrain ruggedness (Figure 3). The western side of the Rif Mountains, where these populations occur, is also one of the wettest areas in Morocco, with annual rainfall exceeding 700 mm. Two small populations in the NE of the Middle Atlas and two populations in the SW of the Middle Atlas also have a high CI (Figure 6) and are located in rugged areas (Figure 3).

The CI suggests the highest conservation priority for the northern populations in the Rif (Jbel Kelti, Tiziren,

National Park of Talassemtane, Issaguen, Bab El Arz, Oursane, and Sidi Boutmim) and in the NE of the Middle Atlas (National Park of Tazzeka) (Figure 6 and Table 3). Other areas in the Middle Atlas (Ouiuane, Timahdit, Ain Kahla, Tigalmamine, and Col du Zad) and in the High Atlas (Assaka) should also be protected. However, our conservation priority analysis did not take into account the genetic and ecological distinctiveness of the populations (May et al., 2011; Moritz, 2002). Further analysis is needed to assess whether populations inhabiting different parts of the range are evolutionarily unique and should be treated as significant conservation units (Crandall et al., 2000; Moritz, 2002). Some populations have high allelic richness, but their overall CI is limited, either because they are located in less rugged areas or because present climate is critical in the context of increasing drought and warming. Forest managers can use populations with high allelic richness such as those in Taffert and Timghilt to improve the genetic diversity of other, less diverse populations through hybridization. However, these translocations should be done after determining that the populations do not represent separate evolutionary units (Crandall et al., 2000; Moritz, 2002).

Some of the areas with high CI are located within the national parks defined by the Moroccan Ministry of Agriculture, which has also delineated three biosphere reserves to balance the conservation of biodiversity and its sustainable use, and plans to add a fourth reserve for Atlas cedar in Middle Atlas (www.eauxetforets.gov.ma/Biodiversite/GestionBiodiversite). Expanding the number of protected areas may be a strategy for conserving biodiversity and endangered species under ongoing global climate change, although some identified modern suitable areas may prove unsuitable in the future (Hannah et al., 2007; Lawler et al., 2020). Identifying potential refugial areas for climate change using model simulations (Albrich et al., 2020; Barrows et al., 2020), ecological complexity at different spatial and temporal scales (Morelli et al., 2020), or integrating climate, topographic diversity, and species-based information (Michalak et al., 2020) or ranking conservation priorities hierarchically across a geographic grid based on other concepts (Carroll et al., 2017; Moilanen et al., 2005) may provide conservation managers with valuable plans to address anticipated threats to plant species. However, our CI is unique in that it combines climate, terrain, and population genetics, which to our knowledge has not been used before, and it can be applied to other regions and species because topographic and climatic data are available worldwide and genetic studies are affordable. This CI can also be used to identify and prioritize conservation areas for populations of multiple species in threatened ecosystems (Cheddadi and Khater, accepted).

CONCLUSIONS

Although all populations that make up the current range of a species are at risk of extinction and therefore all are worthy of conservation, limited resources may force planners to prioritize their efforts in the long term. In this study, we propose a CI to prioritize refugial areas with populations that are genetically adapted to conserve the species and its genetic resources over the long term. Unlike other approaches to species conservation, our CI aims to prioritize areas for conservation based on environmental and genetic data and a climate scenario, which should be a more effective conservation measure in the long term. This CI should be tested and improved with other mountain species using a finer current climate dataset at the microrefuge level and a simulated future climate with higher geographic resolution.

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CONFLICT OF INTEREST

There is no conflict of interest.

AUTHOR CONTRIBUTIONS







Rachid Cheddadi conceived the study, produced the environmental data analyses and figures, and wrote the original manuscript. Rachid Cheddadi, Pierre Taberlet, and Ali Rhoujjati collected the Atlas cedar needle leaves in Morocco. Pierre Taberlet, Eric Coissac, Frédéric Boyer, and Gentile Francesco Ficetola performed the DNA analyses. Salwa el Antry and Jalila Aoujdad provided the most recent estimate of the range of Atlas cedar in Morocco published by the “Service des Etudes et de l’Inventaire Forestier National.” All authors read the manuscript and contributed to its discussion and improvement.

DATA AVAILABILITY STATEMENT

The genetic data is available on FIGSHARE at <https://doi.org/10.6084/m9.figshare.19337117> and the fossil pollen data may be retrieved in the European pollen database (www.europeanpollendatabase.net).

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REFERENCES

- Abel-Schaad, D., Iriarte, E., López-Sáez, J. A., Pérez-Díaz, S., Sabariego Ruiz, S., Cheddadi, R., & Alba-Sánchez, F. (2018). Are *Cedrus atlantica* forests in the Rif Mountains of Morocco heading towards local extinction? *Holocene*, 28(6), 1023–1037.
- Albrich, K., Rammer, W., & Seidl, R. (2020). Climate change causes critical transitions and irreversible alterations of mountain forests. *Global Change Biology*, 26(7), 4013–4027.
- Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, 37, 1407–1413.
- Barrows, C. W., Ramirez, A. R., Sweet, L. C., Morelli, T. L., Millar, C. I., Frakes, N., Rodgers, J., & Mahalovich, M. F. (2020). Validating climate-change refugia: Empirical bottom-up approaches to support management actions. *Frontiers in Ecology and the Environment*, 18(5), 298–306.
- Belkhir, K. (2004). *GENETIX, logiciel sous Windows™ pour la génétique des populations*. Université de Montpellier II.
- Belote, R. T., Dietz, M. S., Jenkins, C. N., McKinley, P. S., Irwin, G. H., Fullman, T. J., Leppi, J. C., & Aplet, G. H. (2017). Wild, connected, and diverse: Building a more resilient system of protected areas. *Ecological Applications*, 27(4), 1050–1056. <https://doi.org/10.1002/eap.1527>
- Bennett, K. D., & Provan, J. (2008). What do we mean by ‘refugia’? *Quaternary Science Reviews*, 27(27–28), 2449–2455.
- Bertrand, R., Lenoir, J., Piedallu, C., Dillon, G. R., De Ruffray, P., Vidal, C., Pierrat, J. C., & Gégout, J. C. (2011). Changes in plant community composition lag behind climate warming in lowland forests. *Nature*, 479(7374), 517–520.
- Birks, H. J. B. (2012). Ecological palaeoecology and conservation biology: Controversies, challenges, and compromises. *International Journal of Biodiversity Science, Ecosystem Services & Management*, 8(4), 292–304.
- Bou Dagher-Kharrat, M., El Zein, H., & Rouhan, G. (2018). Setting conservation priorities for Lebanese flora identification of important plant areas. *Journal for Nature Conservation*, 43, 85–94. <https://doi.org/10.1016/j.jnc.2017.11.004>
- Burrows, M. T., Schoeman, D. S., Richardson, A. J., Molinos, J. G., Hoffmann, A. A., Buckley, L. B., Moore, P. J., Brown, C. J., Bruno, J. F., Duarte, C. M., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Kiessling, W., O’Connor, M. I., Pandolfi, J. M., Parmesan, C., Sydeman, W. J., Ferrier, S., ... Poloczanska, E. S. (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, 507(7493), 492–495.
- Carroll, C., Roberts, D. R., Michalak, J. L., Lawler, J. J., Nielsen, S. E., Stralberg, D., Hamann, A., Mcrae, B. H., & Wang, T. (2017). Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change. *Global Change Biology*, 23(11), 4508–4520.

- Cheddadi, R., Carré, M., Nourelbait, M., François, L., Rhoujjati, A., Manay, R., Ochoa, D., & Schefuß, E. (2021). Early Holocene greening of the Sahara requires Mediterranean winter rainfall. *Proceedings of the National Academy of Science*, *118*(23), 1–7.
- Cheddadi, R., Fady, B., François, L., Hajar, L., Suc, J.-P., Huang, K., Demarteau, M., Vendramin, G. G., & Ortu, E. (2009). Putative glacial refugia of *Cedrus atlantica* deduced from quaternary pollen records and modern genetic diversity. *Journal of Biogeography*, *36*(7), 1361–1371.
- Cheddadi, R., Henrot, A.-J., François, L., Boyer, F., Bush, M., Carré, M., Coissac, E., De Oliveira, P. E., Ficetola, F., Hambuckers, A., Huang, K., Lézine, A.-M., Nourelbait, M., Rhoujjati, A., Taberlet, P., Sarmiento, F., Abel-Schaad, D., Alba-Sánchez, F., & Zheng, Z. (2017). Microrefugia, climate change, and conservation of *Cedrus atlantica* in the Rif Mountains, Morocco. *Frontiers in Ecology and Evolution*, *5*, 1–15.
- Cheddadi, R., Nourelbait, M., Bouaissa, O., Tabel, J., Rhoujjati, A., López-Sáez, J. A., Alba-Sánchez, F., Khater, C., Ballouche, A., Dezileau, L., & Lamb, H. F. (2015). A history of human impact on Moroccan Mountain landscapes. *African Archaeological Review*, *32*, 233–248.
- Christmas, M. J., Breed, M. F., & Lowe, A. J. (2016). Constraints to and conservation implications for climate change adaptation in plants. *Conservation Genetics*, *17*(2), 305–320. <https://doi.org/10.1007/s10592-015-0782-5>
- Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution*, *15*, 290–295.
- Davis, M. B., & Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*(April), 673–679.
- De Barba, M., Miquel, C., Lobreaux, S., Quenette, P. Y., Swenson, J. E., & Taberlet, P. (2017). High-throughput microsatellite genotyping in ecology: Improved accuracy, efficiency, standardization and success with low-quantity and degraded DNA. *Molecular Ecology Resources*, *17*(3), 492–507.
- Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, *17*(2), 1022–1035.
- Ducrey, M. (1981). Action des basses températures hivernales sur la photosynthèse du cèdre et du douglas. *Annales des Sciences Forestières*, *38*(3), 317–329.
- El Hasnaoui, Y., Mhammdi, N., Bajolle, L., Nourelbait, M., Bouimetarhan, I., & Cheddadi, R. (2020). Locating North African microrefugia for mountain tree species from landscape ruggedness and fossil records. *Journal of African Earth Sciences*, *172*, 103996.
- Elsen, P. R., Monahan, W. B., Dougherty, E. R., & Merenlender, A. M. (2020). Keeping pace with climate change in global terrestrial protected areas. *Science Advances*, *6*, eaay0814.
- Esper, J., Frank, D., Buntgen, U., Verstege, A., Luterbacher, J., & Xoplaki, E. (2007). Long-term drought severity variations in Morocco. *Geophysical Research Letters*, *34*(17), 1–5.
- Feddi, N., Fauquette, S., & Suc, J. P. (2011). Histoire plio-pléistocène des écosystèmes végétaux de Méditerranée sud-occidentale: apport de l'analyse pollinique de deux sondages en mer d'Alboran. *Geobios*, *44*(1), 57–69.
- Gao, X., Pal, J. S., & Giorgi, F. (2006). Projected changes in mean and extreme precipitation over the Mediterranean region from a high resolution double nested RCM simulation. *Geophysical Research Letters*, *33*(3), 2–5.
- Gavin, M. C., McCarter, J., Mead, A., Berkes, F., Stepp, J. R., Peterson, D., & Tang, R. (2015). Defining biocultural approaches to conservation. *Trends in Ecology and Evolution*, *30*(3), 140–145.
- Gazol, A., Camarero, J. J., Vicente-Serrano, S. M., Sánchez-Salguero, R., Gutiérrez, E., de Luis, M., Sangüesa-Barreda, G., Novak, K., Rozas, V., Tiscar, P. A., Linares, J. C., Martín-Hernández, N., Martínez del Castillo, E., Ribas, M., García-González, I., Silla, F., Camisón, A., Génova, M., Olano, J. M., ... Galván, J. D. (2018). Forest resilience to drought varies across biomes. *Global Change Biology*, *24*(5), 2143–2158.
- Gillson, L., & Marchant, R. (2014). From myopia to clarity: Sharpening the focus of ecosystem management through the lens of palaeoecology. *Trends in Ecology and Evolution*, *29*(6), 317–325.
- Guisan, A., & Thuiller, W. (2005). Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009.
- Hannah, L., Flint, L., Syphard, A. D., Moritz, M. a., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, *29*(7), 390–397.
- Hannah, L., Midgley, G., Andelman, S., Araújo, M. B., Hughes, G., Martinez-Meyer, E., Pearson, R., & Williams, P. (2007). Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, *5*(3), 131–138.
- Hughes, P. D., Fenton, C. R., & Gibbard, P. L. (2011). Quaternary glaciations of the Atlas Mountains, North Africa. In J. Ehlers, P. L. Gibbard, & P. D. Hughes (Eds.), *Quaternary glaciations - extent and chronology* (Vol. 15, 1st ed., pp. 1065–1074). Elsevier Inc.
- Hughes, P. D., Fink, D., Rodés, Á., Fenton, C. R., & Fujioka, T. (2018). Timing of Pleistocene glaciations in the High Atlas, Morocco: New¹⁰Be and³⁶Cl exposure ages. *Quaternary Science Reviews*, *180*, 193–213.
- Jouzel, J., Masson-Delmotte, V., Cattani, O., Dreyfus, G., Falourd, S., Hoffmann, G., Minster, B., Nouet, J., Barnola, J. M., Chappellaz, J., Fischer, H., Gallet, J. C., Johnsen, S., Leuenberger, M., Loulergue, L., Luethi, D., Oerter, H., Parrenin, F., Raisbeck, G., ... Wolff, E. W. (2007). Orbital and millennial antarctic climate variability over the past 800,000 years. *Science*, *317*(5839), 793–796.
- Karger, D. N., Conrad, O., Böhrner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P., & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Scientific Data*, *4*, 170122.
- Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G. W., Marcantonio, M., & Mucina, L. (2018). Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Annals of Botany*, *122*(6), 927–934.
- Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*(4), 393–404.
- Kübler, D., Hildebrandt, P., Günter, S., Stimm, B., Weber, M., Mosandl, R., Muñoz, J., Cabrera, O., Zeilinger, J., & Silva, B.

- (2015). Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest. *Erdkunde*, 70(1), 19–47. <https://doi.org/10.3112/erdkunde.2016.01.03>
- Ladjal, M., Huc, R., & Ducrey, M. (2005). Drought effects on hydraulic conductivity and xylem vulnerability to embolism in diverse species and provenances of Mediterranean cedars. *Tree Physiology*, 25(9), 1109–1117.
- Lamb, H. F., Gasse, F., Benkaddour, A., El Hamouti, N., van der Kaars, S., Perkins, W. T., Pearce, N. J., & Roberts, N. (1995). Relation between century-scale Holocene arid intervals in tropical and temperate zones. *Nature*, 373, 134–137.
- Lamb, H. F., Roberts, N., Leng, M., Barker, P., Benkaddour, A., & van der Kaars, S. (1999). Lake evolution in a semi-arid montane environment: Responses to catchment change and hydroclimatic variation. *Journal of Paleolimnology*, 21, 325–343.
- Lavorel, S. (1999). Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Diversity and Distributions*, 5, 3–13.
- Lawler, J. J., Rinnan, D. S., Michalak, J. L., Withey, J. C., Randels, C. R., & Possingham, H. P. (2020). Planning for climate change through additions to a national protected area network: Implications for cost and configuration. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794), 20190117.
- Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320, 1768–1771.
- Linares, J. C., Taïqui, L., & Camarero, J. J. (2011). Increasing drought sensitivity and decline of Atlas Cedar (*Cedrus atlantica*) in the Moroccan middle atlas forests. *Forests*, 2(3), 777–796.
- Lindenmayer, D. B., Franklin, J. F., & Fischer, J. (2006). General management principles and a checklist of strategies to guide forest biodiversity conservation. *Biological Conservation*, 131(3), 433–445.
- Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, 462(7276), 1052–1055.
- M'Hirit, O. (1999). Le cèdre de l'Atlas à travers le réseau silva mediterranea "Cedre." Bilan et perspectives. *Forêt Méditerranéenne*, XX(3), 91–100.
- Mattera, M. G., Pastorino, M. J., Lantschner, M. V., Marchelli, P., & Soliani, C. (2020). Genetic diversity and population structure in *Nothofagus pumilio*, a foundation species of Patagonian forests: Defining priority conservation areas and management. *Scientific Reports*, 10(1), 1–13. <https://doi.org/10.1038/s41598-020-76096-0>
- May, S. E., Medley, K. A., Johnson, S. A., & Hoffman, E. A. (2011). Combining genetic structure and ecological niche modeling to establish units of conservation: A case study of an imperiled salamander. *Biological Conservation*, 144(5), 1441–1450. <https://doi.org/10.1016/j.biocon.2011.01.013>
- Michalak, J. L., Stralberg, D., Cartwright, J. M., & Lawler, J. J. (2020). Combining physical and species-based approaches improves refugia identification. *Frontiers in Ecology and the Environment*, 18(5), 254–260.
- Moilanen, A., Franco, A. M., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. (2005). Prioritizing multiple-use landscapes for conservation: Methods for large multi-species planning problems. *Proceedings Biological Sciences*, 272, 1885–1891.
- Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R. M., Stralberg, D., & Thorne, J. H. (2020). Climate-change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, 18(5), 228–234.
- Moritz, C. (2002). Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, 51, 238–254.
- Nolan, C., Overpeck, J., Allen, J. R. M., Anderson, P. M., Betancourt, J. L., Binney, H. A., Brewer, S., Bush, M. B., Chase, B. M., Cheddadi, R., Djamali, M., JohnDodson, Edwards, M. E., Gosling, W. D., Haberle, S., Hotchkiss, S. C., Zheng, Z., & Jackson, S. T. (2018). Past and future global transformation of terrestrial ecosystems under climate change. *Nature*, 361, 920–923.
- Nour El Bait, M., Rhoujjati, A., Eynaud, F., Benkaddour, A., Dezileau, L., Wainer, K., Goslar, T., Khater, C., Tabel, J., & Cheddadi, R. (2014). An 18 000-year pollen and sedimentary record from the cedar forests of the Middle Atlas. *Morocco. Journal of Quaternary Science*, 29(5), 423–432. <https://doi.org/10.1002/jqs.2708>
- Panetsos, K. P., Christou, A., & Scaltsoyiannes, A. (1992). First analysis on allozyme variation in cedar species (*Cedrus* sp.). *Silvae Genetica*, 41(6), 339–342.
- Pautasso, M. (2009). Geographical genetics and the conservation of forest trees. *Perspectives in Plant Ecology, Evolution and Systematics*, 11(3), 157–189.
- Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. Z., Liu, X. D., Miller, J. R., Ning, L., Ohmura, A., Palazzi, E., Rangwala, I., Schöner, W., Severskiy, I., Shahgedanova, M., Wang, M. B., ... Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5(5), 424–430.
- Petit, R. J., El Mousadik, A., & Pons, O. (1998). Identifying populations for conservation on basis of genetic markers. *Conservation Biology*, 12(4), 844–855.
- Petit, R. J., & Hampe, A. (2006). Some evolutionary consequences of being a tree. *Annual Review of Ecology and Evolution*, May, 2013, 187–214.
- QGIS Development Team, 2019. QGIS geographic information system. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>
- Qiao, C.-Y., Ran, J.-H., Li, Y., & Wang, X.-Q. (2007). Phylogeny and biogeography of *Cedrus* (Pinaceae) inferred from sequences of seven paternal chloroplast and maternal mitochondrial DNA regions. *Annals of Botany*, 100, 573–580.
- Ramos, J., Bernal, D., Domínguez-Bella, S., Calado, D., Ruiz, B., Gil, M. J., Clemente, I., Durán, J. J., Vijande, E., & Chamorro, S. (2008). The Benzú rockshelter: A Middle Palaeolithic site on the North African coast. *Quaternary Science Reviews*, 27(23–24), 2210–2218.
- Reille, M. (1976). Analyse pollinique de sédiments postglaciaires dans le Moyen Atlas et le Haut Atlas marocains: premiers résultats. *Ecologia Mediterranea*, 2, 155–170.

- Renau-Morata, B., Nebauer, S. G., Sales, E., Allainguillaume, J., Caligari, P., & Segura, J. (2005). Genetic diversity and structure of natural and managed populations of *Cedrus atlantica* (Pinaceae) assessed using random amplified polymorphic DNA. *American Journal of Botany*, 92(5), 875–884.
- Rhanem, M. (2011). Aridification du climat régional et remontée de la limite inférieure du cèdre de l'Atlas (*Cedrus atlantica* Manetti) aux confins de la plaine de Midelt (Maroc). *Physio-Géo*, 5- (Volume 5), 143–165.
- Riley, S., DeGloria, S. D., & Elliot, R. (1999). A terrain ruggedness index that quantified topographic heterogeneity. *Intermountain Journal of Sciences*, 5(1–4), 23–27.
- Rull, V. (2009). Microrefugia. *Journal of Biogeography*, 36, 481–484.
- Schemske, D. W., Husband, B. C., Ruckelshaus, M. H., Goodwillie, C., Parker, I. M., & Bishop, J. G. (1994). Evaluating approaches to the conservation of rare and endangered plants. *Ecology*, 75(3), 584–606.
- Schröter, D., Cramer, W., Leemans, R., Prentice, I. C., Araújo, M. B., Arnell, N. W., Bondeau, A., Bugmann, H., Carter, T. R., Gracia, C., de la Vega-Leinert, A. C., Erhard, M., Ewert, F., Glendinning, M., House, J. I., Kankaanpää, S., Klein, R. J. T., Lavorel, S., Lindner, M., ... Zierl, B. (2005). Ecosystem service supply and vulnerability to global change in Europe. *Science (New York, N.Y.)*, 310(5752), 1333–1337.
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Steinbauer, M. J., Grytnes, J. A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M., Barni, E., Bjorkman, A. D., Breiner, F. T., Burg, S., Czortek, P., Dawes, M. A., Delimat, A., Dullinger, S., Erschbamer, B., Felde, V. A., ... Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556(7700), 231–234. <https://doi.org/10.1038/s41586-018-0005-6>
- Sutherland, W. J., Adams, W. M., Aronson, R. B., Aveling, R., Blackburn, T. M., Broad, S., Ceballos, G., Côté, I. M., Cowling, R. M., Da Fonseca, G. A. B., Dinerstein, E., Ferraro, P. J., Fleishman, E., Gascon, C., Hunter, M., Hutton, J., Kareiva, P., Kuria, A., MacDonald, D. W., ... Watkinson, A. R. (2009). One hundred questions of importance to the conservation of global biological diversity. *Conservation Biology*, 23(3), 557–567.
- Tabel, J. (2015). Impacts des changements environnementaux passés durant le Quaternaire récent sur la dynamique forestière du Moyen Atlas marocain (Doctoral dissertation, Université Montpellier). 190.
- Tabel, J., Khater, C., Rhoujjati, A., Dezileau, L., Bouimetarhan, I., Carré, M., Vidal, L., Benkaddour, A., Nourelbait, M., & Cheddadi, R. (2016). Environmental changes over the past 25000 years in the southern Middle Atlas. *Morocco. Journal of Quaternary Science*, 31(2), 93–102.
- Taberlet, P., Griffin, S., Goossens, B., Questiau, S., Manceau, V., Escaravage, N., ... Bouvet, J. (1996). Reliable genotyping of samples with very low DNA quantities using PCR. *Nucleic Acids Research*, 24(16), 3189–3194.
- Terrab, A., Hampe, A., Lepais, O., Talavera, S., Vela, E., & Stuessy, T. F. (2008). Phylogeography of north African atlas cedar (*Cedrus atlantica*, Pinaceae): Combined molecular and fossil data reveal a complex quaternary history. *American Journal of Botany*, 95(10), 1262–1269.
- Thakur, S., Negi, V. S., Dhyani, R., Satish, K. V., & Bhatt, I. D. (2021). Vulnerability assessments of mountain forest ecosystems: A global synthesis. *Trees, Forests and People*, 6, 100156.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. a., Peterson, A. T., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427(6970), 145–148.
- Thomas, P. 2013. *Cedrus atlantica*. The IUCN red list of threatened species 2013: e.T42303A2970716. <https://doi.org/10.2305/IUCN.UK.2013-1.RLTS.T42303A2970716.en>
- USGS EROS Archive. Digital Elevation - Global 30 Arc-Second Elevation (GTOPO30). DOI: [10.5066/F7DF6PQS](https://doi.org/10.5066/F7DF6PQS)
- Valencia, B. G., Matthews-Bird, F., Urrego, D. H., Williams, J. J., Gosling, W. D., & Bush, M. B. (2016). Andean microrefugia: Testing the Holocene to predict the Anthropocene. *The New Phytologist*, 212(2), 510–522.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416(6879), 389–395.
- Whittaker, R. H., Levin, S. A., Root, R. B. (1973). Niche, habitat, and ecotope. *The American Naturalist*, 107(955), 321–338. <https://doi.org/10.1086/282837>
- Wright, J. (1952). Pollen dispersion of some forest trees. In *Station Paper 46, United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, Pennsylvania, USA*. 42.
- Zapata, L., Lopez-Saez, J. a., Ruiz-Alonso, M., Linstädter, J., Perez-Jorda, G., Morales, J., Kehl, M., & Pena-Chocarro, L. (2013). Holocene environmental change and human impact in NE Morocco: Palaeobotanical evidence from Ifri Oudadane. *The Holocene*, 23(9), 1286–1296. <https://doi.org/10.1177/0959683613486944>

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