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Original research article

Come rain or come shine, the species richness will decline in the Moroccan mountains

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ABSTRACT

Plant species richness in mountainous regions generally follows a unimodal distribution with lower values at both low and high altitudes in relation to precipitation. In the Atlas mountains, Morocco, plant species richness is currently highest at 800–1200 m elevation, but the extent and altitudinal limits of this species-rich belt have shifted in the past with climate change.

Here, we trace the evolution of pollen taxonomic richness (PTR) as a proxy for plant species richness, with the aim of understanding the relationship with climatic changes over the past 19,000 years, and make some assumptions about future changes in species richness. Past PTR was inferred through an analogy with an extensive modern pollen dataset, and past climatic variables were reconstructed from a fossil record collected in the Middle Atlas, Morocco.

We found that the current PTR distribution in Morocco is more closely associated with precipitation than with temperature. During the last glacial period, both PTR and annual precipitation were low, and the analogs were located at lower altitudes than the altitude of the fossil record. During the early Holocene, the PTR increased by approximately 15%, and the modern analogs were found approximately 600–800 m higher than the analogs of the last glacial period. After 6000 years BP, we observe a steady decline in annual precipitation of approximately 30%, resulting in a species richness loss of approximately 18% and a retreat of the upper boundary of the species-rich belt.

Climate projections suggest that annual precipitation in Northwest Africa will decrease by 20–30% over the next 50 years, an annual amount comparable to that of the last glacial period, but under much warmer conditions and in a significantly shorter time. Such a decline in precipitation could result in an unprecedented loss of plant species richness of approximately 15% in just a few decades and put 35% of the protected areas at risk. The forested mountains above 1600 m could then resemble the treeless and less diverse steppes found at higher altitudes above today's tree line.

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1. Introduction

Species richness is one of the most commonly used criteria for assessing biodiversity and its changes over space and time (Graham et al., 2014; Shapcott et al., 2017; Steinbauer et al., 2018; Wiens et al., 2006). There are currently international initiatives to conserve species in protected areas (Negacz et al., 2022), biosphere reserves and Key Biodiversity Areas (KBA) (BirdLife, 2020). These initiatives are crucial for species conservation, but some current protected areas may prove unsuitable in the future given the rate and magnitude of climate change (Lawler et al., 2020). It is therefore essential to assess the impact of climate change on species richness over time, both within and beyond the boundaries of protected areas.

Worldwide, mountains are considered a reservoir of biodiversity (Perrigo et al., 2020) with a higher species richness than lowlands (Rahbek, 1995; Grytnes and Vetaas, 2002; Pellissier et al., 2012). In Morocco, mountains account for more than 35% of the total land area and harbor up to 50% of native endemic plant species (Rankou et al., 2013). The vegetation communities of Morocco show a topoclimatic distribution with dry and warm herbaceous and thorny shrub species in the lowlands up to 700–800 m asl (infra-mediterranean), denser forests (thermo-mediterranean) up to 1400 m asl and mixed forests (meso- and supra-mediterranean) up to the tree line at 2200 m above sea level, followed by steppes with scarce trees at altitudes above 2200 m above sea level (oro-mediterranean) (Benabid, 1985, 1982). Forests across North Africa are currently affected by a drought unprecedented in the last nine centuries (Esper et al., 2007; Touchan et al., 2011; Linares et al., 2011). Atlas cedar (*Cedrus atlantica*) forests in the Rif Mountains have experienced 75% dieback over the past five decades, which has caused a >100 m increase in their lower altitudinal boundary (Cheddadi et al., 2017) and resulted in a loss of plant species richness.

In mountainous regions, species richness exhibits a unimodal pattern with altitude, with the highest values occurring at mid-elevations (Rahbek, 1995), across a range of different latitudes and climatic zones (Rahbek, 1995, Pellissier et al., 2012, Grytnes and Vetaas, 2002). Similarly, in North Africa today, the highest plant species richness occurs in an ecotone between 800 and 1200 m that overlaps with thermo- and meso-Mediterranean vegetation types (Benabid, 1985, 1982), where many KBAs and national parks are established (Fig. 1). The belt with the highest species richness at medium altitude can also occur at different altitudes in other mountainous regions (Rana et al., 2019), e.g. in the Himalayas between 1500 and 2600 m (Grytnes and Vetaas, 2002) or in the Alps between 1400 and 2000 m (Pellissier et al., 2012).

To assess the long-term importance of these protected areas and develop climate-adapted conservation strategies, it is crucial to understand how the altitudinal range of conditions favoring high species richness will change as a result of climate change. Palaeoecological records contain a wealth of information on the occurrence and distribution of plant species in the past, as well as on climate, allowing us to assess a broader range of natural, climate-induced changes in species richness in time and spatially (Willis et al., 2010; Dawson et al., 2011; Gillson and Marchant, 2014). They can provide us with a valuable assessment of the temporal and spatial evolution of plant species richness under different climate configurations, which can help us to better assess the future relevance of already established protected areas. Historical data must be used to develop effective strategies for the long-term conservation of plant species richness.

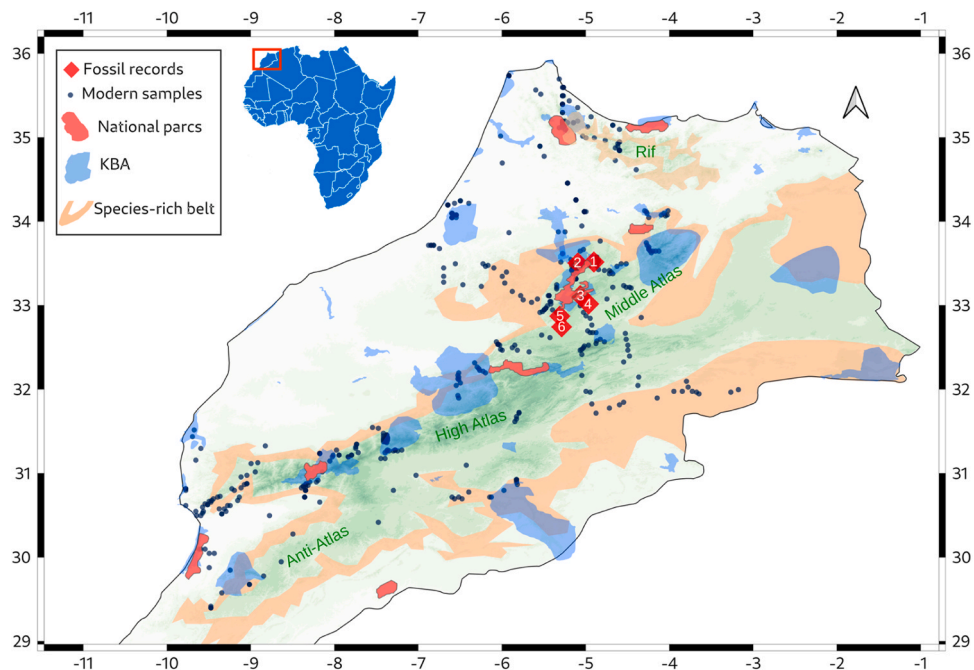


Fig. 1. Modern biodiversity areas and pollen datasets with Key Biodiversity Areas (KBA) (BirdLife, 2020), national parks, species-rich belt (800–1200 m), modern pollen samples, and fossil pollen records in the Middle Atlas, Morocco.

In the present study, we have used an extensive set of modern pollen samples as recent observations to estimate the spatial distribution of pollen taxonomic richness (PTR) in northern Morocco, as well as a unique set of fossil pollen records from the Middle Atlas Mountains covering the last 24,000 years. The latter period covers very different climatic periods between the cold and dry Last Glacial Maximum and the warmer and wetter early to mid-Holocene. Using the modern and fossil datasets, we estimated the past ranges of PTR in relation to changes in climate and inferred possible future changes in species richness. Our data show that the expected climate changes in the Mediterranean region will clearly lead to a noticeable decline in plant species richness in the Atlas mountains.

2. Materials and methods

2.1. Approach

Our method entails combining modern and fossil datasets in order to analyze the variations in plant species richness across Morocco over time. By employing a contemporary pollen dataset, as illustrated in Fig. 1, we determine the PTR, which serves as a proxy for plant species richness, at different altitudes. This modern dataset provides us with information on the geographical distribution of plant species richness. To determine the current relationship between PTR and climate, we utilize a contemporary dataset of climate.

In order to assess the relationship between Late Quaternary fluctuations in PTR and climate shifts, while preventing circular reasoning, we employ two separate datasets. We infer the past PTR from the modern pollen samples by selecting the best analogs for the fossil pollen samples and reconstruct the past climate changes from the fossil record. The modern pollen samples provide us with the analogous PTR of the modern sample and its related elevation to each fossil sample. The resulting PTR time series from the modern dataset allows us to reconstruct the altitudinal changes of each fossil sample and its richness and ultimately anticipate the potential future changes in richness under expected climate changes.

2.2. The pollen datasets

The dataset of modern pollen used in this study consists of 400 samples collected throughout Morocco (Fig. 1), of which 284 are from Saadi and Bernard (1991) and 116 from unpublished data (see Acknowledgments). The dataset includes 175 pollen taxa and covers most of the lowland and mountain ecosystems from sea level to 2550 m asl. The modern samples allowed us to estimate the pollen taxonomic richness (PTR) in Morocco and served as a reference database to find the closest modern analogs to each fossil sample using a Euclidean distance between the two pollen assemblages. The mean elevation of the 10 closest modern analogs is considered to be the elevation of the ecosystem that best corresponds to the ecosystem of the site where the fossil pollen sample was deposited (supplementary figure 1).

Fossil pollen data are more abundant in mountainous regions than in lowlands due to the presence of long-lasting wetlands (lakes, swamps, peat bogs) that accumulate sediments that serve as historical archives for tracing the composition of ecosystems over time. The original fossil pollen dataset includes six previously published records collected in the Middle Atlas (Fig. 1 & 2) in Lake Hachlaf at 1700 m (Tabel, 2015), in the Ras El Ma swamp at 1633 m (Nour El Bait et al., 2014), in Lake Tifounassine at 1921 m (Tabel, 2015), in Lake Sidi Ali at 2080 m (Lamb et al., 1999), in Lake Tigalmamine at 1626 m (Lamb and van der Kaars, 1995) and in the Ait Ishou swamp at 1661 m (Tabel et al., 2016). We used this fossil dataset to reconstruct past climate changes in a mountainous region covering an elevation range between ~1600 m and ~2000 m and an area of about 90 km long and 40 km wide (Fig. 2). An important question is whether our six pollen records show similar changes in plant composition over time so that we can combine them into a single record that covers the entire area where they were collected.

The six pollen records form a local composite image of a regional time-series similarity. The pollen percentages of their common

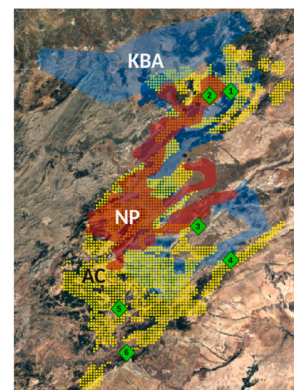


Fig. 2. Altitudinal profile and distance between the locations where the six pollen records were collected in the Middle Atlas. The small map shows the geographical location of the six records: (1) lake Hachlaf, (2) Ras El Ma swamp, (3) Lake Tifounassine, (4) Lake Sidi Ali, (5) Lake Tigalmamine, and (6) Ait Ishou swamp. NP (red area)=Ifrane National Park, KBA (blue area)= Key Biodiversity Area and AC (yellow area)= Atlas Cedar populations.

plant taxa exhibit varying amplitudes and rates of change over the period in which they occur. As a result, each pollen record, which documents local changes, is not aligned exactly with the other records in the same region and on the same timeline, which may give the impression that local variations make them different enough not to be combined into a single regional record. To assess the degree of similarity between the six records, we used a Dynamic Time Warping (DTW) approach from the R package *dtw* (Giorgino, 2009), using the normalized Euclidean distance between each record for the eleven dominant taxa. The DTW method is capable of efficiently matching time series and detecting patterns of changes where traditional data aggregation techniques cannot (Hegg and Kennedy, 2021). To account for variability in the length of each pair of records, we normalized the distance by dividing it by the sum of the lengths of each two sequences and using the upper triangular matrix to avoid null distances and redundancy due to the symmetry of the distances. DTW is a classic method for comparing time-dependent sequences with different lengths. It adjusts the sequences to align the most similar points and establish the optimal matches between points of differing sequences. The main idea is to define a cost matrix based on the distance between data points. Dynamic programming is used to find the optimal alignment by minimizing the total cost, which allows flexible alignment. DTW outputs the cumulative distance between time series, which provides a more adaptable approach for comparing time series data compared to conventional alignment methods.

2.3. Pollen Taxonomic Richness (PTR) and analogs

We define the PTR as the number of different pollen grains identified in a pollen sample. The PTR is a simple count of pollen taxa without evaluating the number of their occurrences in a sample. The identification of pollen grains is often limited to the genus or family level, which can be seen as a limitation for estimating the species richness of plants. However, pollen grains identified at the genus or family level may originate from the same or different plant species if they occur in the ecosystem, so we consider that pollen grains represent a minimal "image" of the species richness of an ecosystem. Despite the known challenges in identifying pollen grains to species level, we assume that changes in the PTR should reflect changes in the species richness of the ecosystem from which they originate. To estimate the PTR of our modern pollen dataset (Fig. 5A), we used rarefaction analysis (Birks and Line, 1992), which is an appropriate method for pollen samples because they are extracted from the sediment, identified and counted according to a standardized procedure (Tipper, 1979).

2.4. Pollen-based climate reconstruction

To reconstruct past climate variables, we apply a statistical method that relies on the present-day distribution of plant species and associated climate to determine the prevailing climate for each pollen taxon in a fossil sample. Based on our palynological, botanical and ecological knowledge of the study area, we first assign fossil pollen taxa identified to genera to modern plant species, and we exclude those identified to the family level. We have a database of modern geographical distributions of plant species from different floras (Cheddadi and Khater, 2016) and the associated climate variables from the WORLDCLIM database (Hijmans et al., 2005). Once the fossil pollen grains are assigned to modern plant species, we derive their distribution ranges and the associated climate variable from the database. We then calculate the median range of the focal climate variable for all fossil pollen taxa assigned to modern plant species. In the present study, the focal climate variables are annual precipitation (Pann) and annual mean temperature (Tann). The climate range of a species may be defined as the range of the focal climate variable where the species occurs today. The determined climate value is the weighted mean (\bar{T}_m) of the medians of the climate range (M) of n pollen taxa identified in a fossil sample (T1 to Tn) as follows:

$$\bar{T}_m = \sum_{i=1}^n w_i M(T_i) \text{ with } \sum_{i=1}^n w_i = 1$$

Pollen percentages are used as normalized weights ($0 < w <= 1$). We exclude pollen grains from aquatic and anthropogenic plants and all taxa with an occurrence of less than 1% of the total pollen sum ($w > 0$) because they may originate from plants that are outside the local ecosystem.

To reduce bias and estimate uncertainty for each climate variable and fossil sample, a jackknife procedure was used in which the climate estimate is iterated by omitting one taxon as many times as the number of taxa in each fossil sample at each iteration. After completing the jackknife procedure, we calculate the median of all weighted means for each climate variable to obtain the final climate value of the focal variable and its associated uncertainty. The latter is equal to the median of the standard deviations of the iterations.

This approach assumes that there is a large overlap between the present and past climate of the plant species, at least in the period under study. We refute the hypothesis that any plant species in our Mediterranean study area has inhabited a specific climatic niche in the last 19,000 years that does not overlap with its current distribution.

The accuracy of our pollen-based climate reconstruction method was validated by comparing the reconstructed climate variables from a modern pollen dataset with the WorldClim climate data (Cheddadi et al., 2021). All statistics and database queries (MySQL) were performed using R software version 4.2.2 (R Core Team, 2022) with the libraries Akima (Akima, 1978), RMySQL (Ooms et al., 2019), Zoo (Zeileis and Grothendieck, 2005) and Stats (R Core Team, 2022).

3. Results

The six pollen records in the Middle Atlas share between 26% and 75% (Table 1) of the common pollen taxa, including eleven dominant trees, shrubs and herbs (*Artemisia*, Asteraceae, Brassicaceae, *Cedrus atlantica*, Chenopodiaceae, Cichorioideae,

Gramineae, *Helianthemum*, *Olea europaea*, *Pinus* and *Quercus* evergreen) occurring at all sites. However, the number of pollen samples analyzed in each pollen record varies. The data contained in the six records provides a comprehensive overview of PTR changes that spans a minimum of 12,000 years. Among these records, four of them cover the period of the past 15,000 years, and only Sidi Ali extends back 7000 years (as depicted in Fig. 4).

In addition to the relatively high number of common taxa (26–75%) in the six records, the small cumulative distances determined by DTW (Fig. 3) show that there is a high degree of similarity over the study period for ten of the eleven common taxa. To make this more convincing it would be required to restrict the analysis to the time overlapping parts of the time series and show the alignment plots between datasets. After evaluating the degree of similarity between the six pollen records we combined them into one regional record.

With the exception of the Gramineae, a ubiquitous family, the great similarity between the six pollen records allows them to be grouped into a single record that covers both their collective time spans and the large area in which they were collected. To combine the six sequences into a single pollen record, we assembled the samples based on their respective ages. The ages of the samples were obtained from an age model based on radiometric dating and developed by the authors of the sequences.

The new pollen sequence includes 111 pollen taxa identified in a total of 397 pollen samples and spans 24,000 years (Fig. 4). We focused on the last 19,000 years BP because only one pollen record (Ait Ishou) extends back to 24,000 years BP and has only one calibrated ^{14}C date ($21,276 \pm 80$).

From the modern dataset of 400 modern pollen samples, we obtained the current spatial distribution of PTR, which varies between 22 and 41 pollen taxa from sea level to 2400 m (Fig. 5A). The modern PTR shows a unimodal distribution as a function of altitude, with the highest values between 800 and 1200 m altitude (Fig. 5A). This pattern is consistent with local field observations of ecosystem composition (Benabid, 1982, 1985) and is similar to the altitudinal distribution of plant species richness in other mountain regions (Grytnes and Vetaas, 2002; Sanchez-Gonzalez and Lopez-Mata, 2005; Pellissier et al., 2012). These similarities in current PTR and plant species richness allow us to use PTR as a proxy for species richness.

To estimate the past PTR we used the modern pollen dataset to seek analogous pollen assemblages to the fossil samples, which provides us with the past species richness and its related elevation. Thus, the reconstructed past PTR from the modern dataset shows low values during the last glacial period and then after 6000 years BP (Fig. 5B). The highest PTR occurs during the early to mid-Holocene (Fig. 5B) with values that correspond to those of the modern belt with the highest PTR between 800 and 1200 m elevation (Fig. 5A).

To determine which variable is best correlated with species richness in Morocco we compared the modern PTR with altitude, annual precipitation (Pann) and annual mean temperature (Tann) (Fig. 6). The current climate variables were obtained from the WORLDCLIM database (Hijmans et al., 2005) and interpolated onto the locations of the modern pollen samples using a linear interpolation. We find that Pann is more strongly correlated with PTR ($r=0.50$) than Tann ($r=-0.15$) or altitude ($r=0.14$) (Fig. 6). In contrast to Tann, which is strongly anticorrelated with altitude ($r=0.79$), PTR and Pann are not correlated with altitude ($r=0.16$ and 0.14 , respectively).

4. Discussion

4.1. Present-day relationship between climate and species richness

The distribution of species richness across altitudinal gradients is influenced by several abiotic variables, including productivity, sun exposure, topography ruggedness and climate. The latter is an important local and regional factor (Rahbek et al., 2019; Antonelli et al., 2018). A standardized monitoring network across the major mountain ranges of Europe has shown a decline in species richness over a short period (2001–2008) on the mountain peaks around the Mediterranean, where increased temperatures have led to greater water stress. In contrast, in the Alps, which are higher in altitude and latitude than the Mediterranean mountains, species richness increases at high elevations due to an increase in mean annual temperature (Pauli et al., 2012; Grabherr et al., 1994). In California's Sierra Nevada, a mountain range with an elevation gradient similar to that of the Alps, simulations of the interaction between disturbance and projected climate change indicate that tree species richness may be decreasing (Liang et al., 2017). At the global scale, biomes, such as the warm mixed forest and the grassland/steppe, which occur in the Mediterranean, are expected to undergo a species extinction rate between 15.7% and 20.3% by 2050, while the tundra, and the boreal and tropical forests could lose less than 4% (Thomas et al., 2004). Overall, species richness does not appear to have shown a clear increasing or decreasing trend in recent decades

Table 1

Number of common pollen taxa that occur in each pair of sites.

	Hachlaf	Ras el Ma	Sidi Ali	Tifounassine	Tigalmamine	Ait Ishou
Hachlaf	37					
Ras el Ma	20	61				
Sidi Ali	19	16	47			
Tifounassine	28	21	19	38		
Tigalmamine	20	21	30	23	40	
Ait Ishou	28	20	16	25	19	32

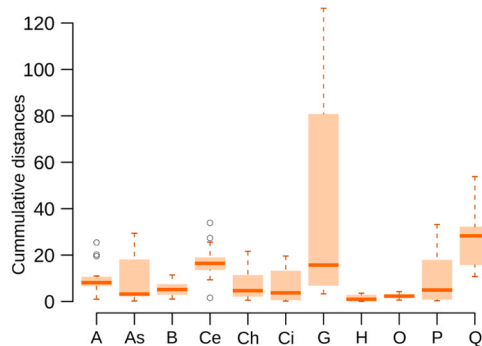


Fig. 3. Boxplots of cumulative normalized distances between the eleven dominant taxa in the six pollen time series. A=Artemisia, As=Asteraceae, B=Brassicaceae, Ce=Cedrus atlantica, Ch=Chenopodiaceae, Ci=Cichorioideae, G=Gramineae, H=Helianthemum, O=Olea europaea, P=Pinus and Q=Quercus.

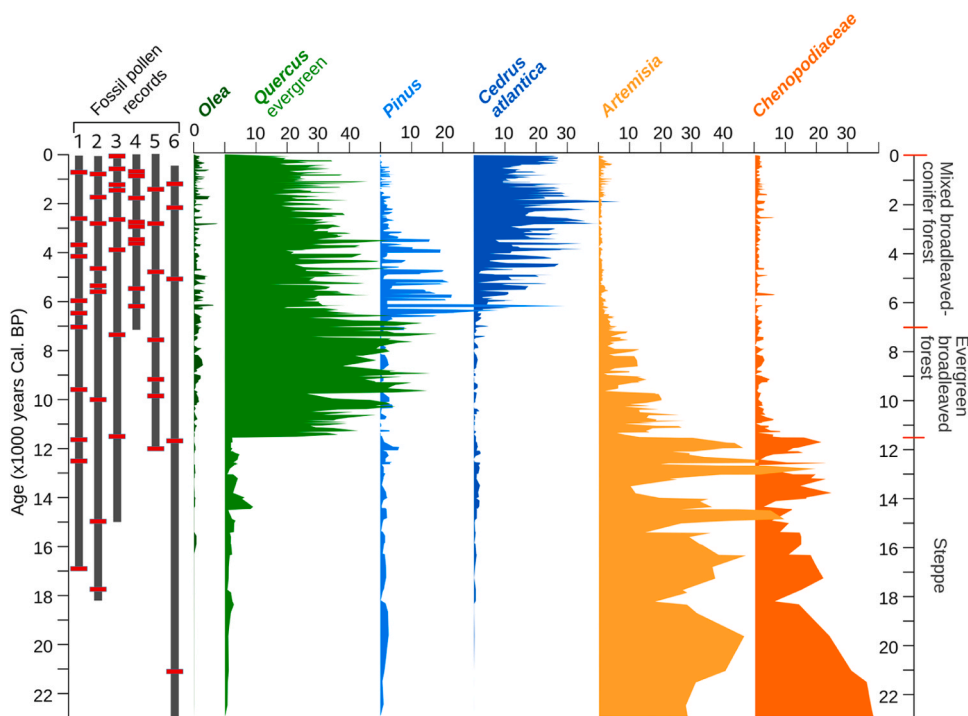


Fig. 4. Synthetic pollen diagram from the six combined fossil records in the Atlas Mountains, Morocco. This synthetic pollen diagram shows the percentage of pollen (x-axis) from six taxa that characterize the major ecosystem changes from a steppe during the last ice age to a Mediterranean broadleaved evergreen and coniferous forest in the late Holocene. The six numbered vertical black bars represent the time span covered by each pollen record (from 1 to 6 above, see Fig. 1 & 2 for their geographical locations), and the red bars are the radiocarbon-dated samples in each record.

and areas (Chapin et al., 2000; Vellend et al., 2013), and it remains unclear whether it will rise or fall in all mountains in the near future, as there are considerable regional biotic and abiotic differences (Grabherr et al., 1994; Engler et al., 2009; Holzinger et al., 2008; Pauli et al., 2012).

The PTR in Morocco shows a stronger relationship with precipitation than with temperature (Fig. 6). The correlation between PTR, as a proxy for species richness, and precipitation has been observed in other areas, and is particularly evident in warm regions where plants are not limited by energy availability (Hawkins et al., 2003), such as North Africa. Outside the Mediterranean region, strong positive correlations have been found between altitudinal diversity of animals and temperature, where temperature is the dominant climatic factor (McCain, 2009). However, at local and regional scales and over different time periods in the Mediterranean region, precipitation may be a more significant factor in explaining changes in species richness. Our study aims to investigate these relationships at different temporal and spatial scales by considering changes in species richness in response to different climate variables in Morocco.

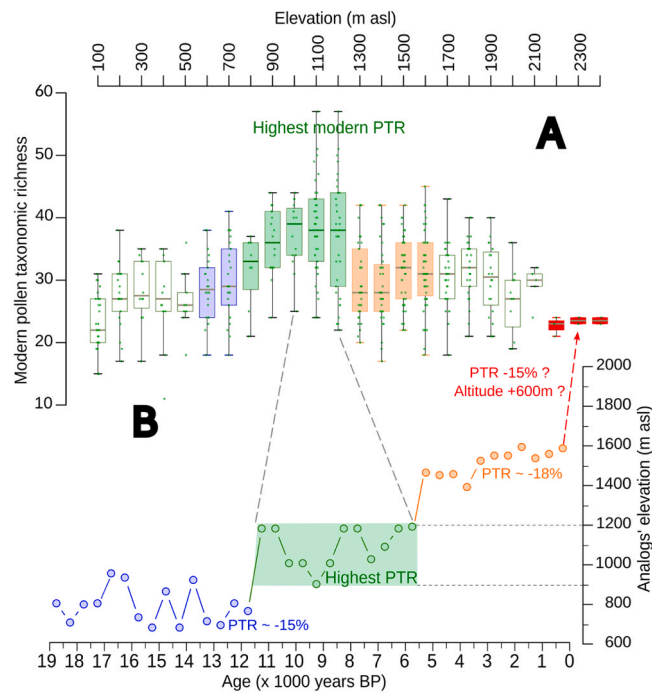


Fig. 5. Changes in the pollen taxonomic richness (PTR) as a function of altitude and time. (A): Modern PTR along an altitudinal gradient for every 100 m of elevation between sea level and 2400 m. Boxplots show medians and quantiles (0, 25, 75 and 100%) of PTR of 400 modern pollen samples (see Fig. 1 for geographical distribution). (B): Elevation of the modern pollen samples analogous to the fossil samples (in a time step of 500 years over the last 19,000 years). The blue, green, and orange circles are the median values of the 397 fossil pollen samples. The green area corresponds to the altitudinal range of the early to mid-Holocene where the modern samples in (A) have the highest PTR.

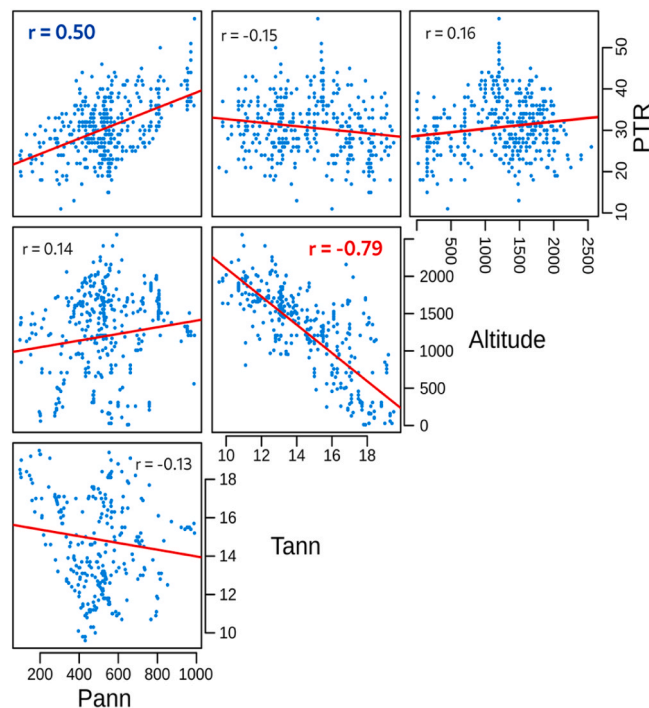


Fig. 6. Pearson pairwise correlation between current pollen taxonomic richness (PTR), annual precipitation (Pann in mm), mean annual temperature (Tann in °C) and altitude (in m). All p values are <0.001.

4.2. Past species richness changes

Between the end of the last ice age and the Holocene optimum the pollen-based reconstructed precipitation in the Middle Atlas mountains reveals a significant increase in annual precipitation of approximately 30%, which occurred around 9000 years ago (Fig. 7). This increase in moisture during the post-glacial transition contributed to a gain of about 15% in PTR (Fig. 5B). The cedar forests, where the six fossil records were collected, are located between 400 and 800 m above the upper boundary of the modern species-rich belt, which is today 1200 m above sea level. The high PTR (Fig. 5B) during the mid-Holocene shows that the studied region in the Middle Atlas was within the species-rich belt and suggests that the upper boundary of the belt was at least 400 m higher than its current altitude during that time.

The early Holocene was about 6°C warmer than the last ice age (Fig. 7), which corroborates well with the global annual temperature record of the last 24,000 years (Osman et al., 2021). Both records exhibit a comparable amplitude during the transition between the last ice age and the early Holocene, as well as low variability throughout the Holocene period. During the early and mid-Holocene, the entire North African continent was wetter than it is today (Shanahan et al., 2015). This period, known as the African Humid Period (DeMenocal et al., 2000), was responsible for the "Green Sahara" (Pausata et al., 2020), which featured extensive lakes (Quade et al., 2018) and a diverse array of tropical and Mediterranean plant species in an area that is now a barren desert (Watrin et al., 2009). The precipitation levels throughout Northwest Africa during the early Holocene were recorded at all elevations, from sea level (Tierney et al., 2017) to the Atlas Mountains (Cheddadi et al., 2021), with a significant increase in precipitation in the lowlands compared to the mountains. Our PTR record also reveals a substantial increase in response to the post-glacial increase in precipitation, which supports the notion that the African Humid Period had a substantial positive impact on plant species richness in North Africa.

The decrease in annual precipitation observed around 6000 years ago and afterward was approximately 30%, resulting in pollen assemblages similar to those of modern pollen samples collected at elevations ranging from 1300 m to 1600 m, where the PTR was approximately 18% lower than that during the early Holocene (Fig. 5B). The late Holocene was approximately 1–2°C cooler than the early Holocene (Fig. 7), but the main difference between these two periods is the aridification trend during the late Holocene, which is well documented with regards to its impact on Mediterranean forest cover (Ramos-Roman et al., 2018). Although the flora was different, the PTR of the late Holocene was comparable to that of the last glacial period. However, during the last glacial period,

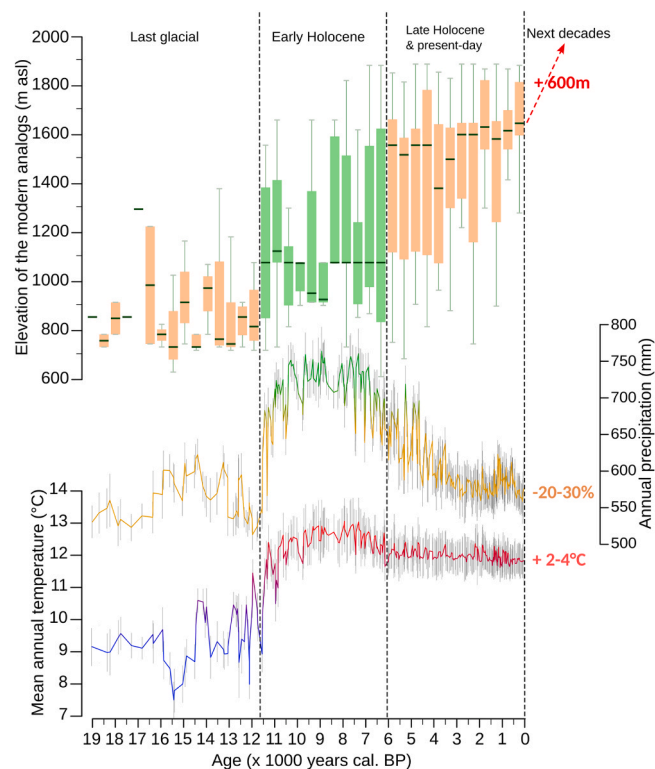


Fig. 7. Past, present and future trends in species richness. The upper boxplots show the elevations of the 10 best modern analogs of the fossil pollen samples. The two lower curves illustrate annual precipitation (green and orange) and mean annual temperature (red and blue). This figure shows that if precipitation decreases by 20–30% in the coming decades (Gao et al., 2008; Ozturk et al., 2015; Gutiérrez et al., 2021), the current forests of the Atlas Mountains might resemble the steppes found today at elevations above 2000 m, where species richness is 15% lower.

modern analogs were located around 800 m, whereas during the late Holocene, they may have been found between 1400 and 1600 m.

This temporal and spatial understanding of how plant species richness responds to climate change highlights the importance of fossil pollen archives for assessing the impact of past climate change and can provide insight into how future plant species richness may change in response to projected climate change.

4.3. Potential future species richness changes

Currently, the prevalent threat to Moroccan forests is drought (Esper et al., 2007; Touchan et al., 2011; Linares et al., 2011). Given the observed significant relationship between precipitation and PTR (Fig. 6), we expect that the frequency and duration of drought over recent decades and their trend toward even drier conditions in northwestern Africa (Touchan et al., 2011) will have a greater impact on species richness than the increase in temperature. The expected warming of 2–4°C over the next four decades in the Mediterranean region (Gao et al., 2008) will result in a mean annual temperature that is approximately 2°C higher than that of the early Holocene, which will enhance the drought effect. Annual precipitation is expected to decrease by approximately 20–30% (Gao et al., 2008; Ozturk et al., 2015; Gutiérrez et al., 2021), which is equivalent to the decrease recorded during the late Holocene. This projected decrease in annual precipitation could lead to a decline in species richness of approximately 15% (Fig. 7), especially at altitudes where key threatened species such as the Atlas cedar and the Moroccan fir (*Abies pinsapo*) occur today and form rather dense forests. Our estimated plant species richness decline in the Atlas Mountains, where warm mixed coniferous forests predominate, corresponds well to the predicted percentages (between 15% and 20%) of species threatened with extinction in these biomes (Thomas et al., 2004).

According to model simulations, the geographical range of the Atlas Cedar has decreased by approximately 75% and its lower limit has risen by at least 100 m over the past 50 years due to the persisting drought (Cheddadi et al., 2017). With the projected additional water stress, the species richness of the forested regions in the Atlas and the Rif mountains is expected to resemble that of the barren steppes at elevations above 2200 m, which presently serves as the tree line. If this scenario continues, about 35% of the key biodiversity areas and national parks situated in or near the region (Fig. 1) boasting the highest species richness may find themselves partially or entirely unsuitable for species preservation, primarily due to persistent water stress.

These insights must be used to assess the relevance of planned national parks and reserves and improve future conservation efforts. The conservation of species in the North African mountains is an immediate challenge that requires the identification of areas of high species richness threatened by climate, as shown in this study, the improvement of their conservation strategies, and the development of a network of new protected areas where species can migrate and spread to maintain genetic diversity. In line with Cheddadi et al. (2022) recommendations, assessing the mountain topography for potential suitable and stable microclimates, evaluating the adaptive capacity of plant species on the ground, and taking into account anticipated regional climate changes are essential for determining the location of areas to be protected.

It is suggested that all current protected areas, including KBAs, national parks, and biosphere reserves that are situated in or bordering mountain forests, be given top priority for preservation. Additionally, it is recommended that new protected areas be established close to the tree line to enable the growth of seedlings in the absence of human interference. Optimally, both existing and new protected areas ought to be organized in a geographical network that enables the dispersion of seeds and the exchange of genetic material between them, thereby enhancing the genetic diversity of species and their capacity to adapt over the long term.

5. Conclusions

The Mediterranean area, which encompasses Northwest Africa, has experienced considerable shifts in precipitation over the last 19,000 years, which has had an impact on the distribution of species at different elevations. It is essential to understand the connection between past climate change and species diversity in order to develop effective conservation strategies. Our paleoecological data demonstrate that species diversity varies over time and space in response to changes in precipitation, with these changes occurring over several millennia, allowing plant species to migrate to more suitable areas.

However, the predicted decrease in precipitation is expected to happen in a much shorter time frame and will fall below the levels experienced over the last 19,000 years. This rapid pace of contemporary climate change will result in a decline in plant species diversity and will transform forest ecosystems at elevations above 1600 m into treeless steppes, a habitat type that is currently found beyond the tree line at 2200 m. While our study does not provide a quantitative estimate of future plant species diversity, it does indicate a trend of loss under drier conditions, with North Africa's forested ecosystems potentially losing approximately 15% of their plant species diversity.

CRedit authorship contribution statement

Avner Bar-Hen: Writing – review & editing, Methodology. **Nick Marriner:** Writing – review & editing. **Matthew Hurteau:** Writing – review & editing, Conceptualization. **David Kaniewski:** Writing – review & editing. **Rachid Cheddadi:** Writing – review & editing, Writing – original draft, Validation, Methodology, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rachid Cheddadi reports administrative support was provided by Centre National de la Recherche Scientifique. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Authors contribution

R.C. conceived the study with input from all co-authors. RC developed the methodology and wrote the original draft of the manuscript. D.K., N.M. and M.D.H. reviewed and edited the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02986](https://doi.org/10.1016/j.gecco.2024.e02986).

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