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**Holocene palaeoecological archives of Eastern Mediterranean plant diversity:  
past, present and future trends**

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**Abstract**

The Mediterranean Basin is an environmental change hotspot that, relative to other regions of the world, is forecasted to experience a significant shift in biodiversity due to multiple factors such as climate change and agricultural intensification. Within this framework, the Eastern Mediterranean region is projected to face a temperature rise of  $\sim 3.5\text{-}7^\circ\text{C}$  by 2070-2099 which will result in severe heat stress and freshwater scarcity, along with increased human impacts due to pronounced demographic growth. To assess the impact of environmental and human pressures on plant diversity, we studied the evolution of this major constituent of biodiversity in the Eastern Mediterranean over 8000 years. Our analysis demonstrates that plant diversity has been impacted by long-term (e.g. multi-millennial scale) changes in temperature, precipitation and anthropogenic activities. We identified a tipping point for each of these drivers, showing that Eastern Mediterranean plant diversity has already exceeded its tipping point for precipitation (threshold:  $376\pm 17$  mm for winter), while it has already attained its critical threshold for temperature (threshold:  $1.33\pm 0.5^\circ\text{C}$ ) and anthropogenic activities (threshold:  $-1.05\pm 0.4$  - low to medium pressures). This suggests that the region's vegetation will probably progressively give way to species that are better suited and more resilient to the changing environmental conditions.

**Keywords:** Plant diversity, Climate, Human impact, Holocene, Eastern Mediterranean

## 1. Introduction

The Mediterranean is the world's third most important hotspot for plant diversity, hosting no less than 25,000 vascular plant species, of which about 5500 are endemic (Thompson, 2020; Lopez-Alvarado and Farris, 2022). Nonetheless, it has long been acknowledged that Mediterranean vegetation is extremely vulnerable to global changes, rendering it one of the most imperiled ecosystems (Sala et al., 2000; Fischer and Schär, 2010). The region is expected to experience the greatest proportional change in biodiversity by 2100 due to its high sensitivity to both land-use changes (José-María et al., 2010; Tarifa et al., 2021) and climate pressures (IPCC, 2022a; Sala et al., 2000; Underwood et al., 2009; Newbold et al., 2020). The Southern and Eastern Mediterranean regions have been identified as areas of particular concern by both the IPCC (2014, 2022b) and scientific studies (Lelieveld et al., 2012, 2014, 2016). By 2100, projected mean warming for the Mediterranean could be  $3^\circ\text{C}$  (RCP4.5 scenario) to  $9^\circ\text{C}$  (RCP8.5 scenario) warmer than the beginning of the 21<sup>st</sup> century (Bucchignani

et al., 2018; Ozturk et al., 2018; IPCC, 2022b). Based on current trends, it is projected that the frequency and duration of heatwaves will significantly increase, along with a rise in the annual number of extremely hot and dry days (Driouech et al., 2020; Varela et al., 2020). Moreover, mounting population pressures (Lemaitre-Curri, 2020) coupled with the intensification of land-use practices such as intensive agriculture (José-María et al., 2010), are likely to exacerbate the already existing stress on plant diversity, and thereby further accelerate its decline. The Eastern Mediterranean's plant diversity is particularly vulnerable due to the existing water deficits (Moilanen and Mroueh, 2010), above normal temperature rise (values of up to 0.68°C/decade; Salameh et al., 2019) and a positive demographic trend which, in some countries (e.g. Syria, Egypt), exceeds the Mediterranean's average birth rate (Lemaitre-Curri, 2020). The gradual exacerbation of climate change, coupled with the intensification of agricultural practices to meet the demands of a burgeoning population, is poised to significantly impact the plant diversity of the Eastern Mediterranean region.

Understanding the plurisecular relationship between climate, agriculture and plant diversity in the Eastern Mediterranean region is therefore key to assessing how ecosystems will be altered in the future. Evaluations of historical plant diversity are notably limited in the scientific literature; however, research has demonstrated that pollen is a pertinent tool for examining the enduring development of both biological diversity and functional diversity across geographic regions (Matthias et al., 2015; Chevalier et al., 2020; Leontidou et al., 2021; Hornick et al., 2022; Adeleye et al., 2023). Trends in pollen-derived plant diversity can therefore be reconstructed (Foster et al., 2010; Ivory et al., 2018; Florenzano, 2019; Chevalier et al., 2020; Coussin et al., 2023), furnishing insights into how biodiversity plays out in the face of increasing climate and anthropogenic pressures.

This study is centered on a comprehensive assessment of plant diversity in the Eastern Mediterranean region, with a holistic approach that does not single out specific ecosystems or plant groupings. This approach is justified by the fact that both current and anticipated future changes are exerting pressures on all plant species across the region. We probe the tolerance range and tipping points for plant diversity in relation to three primary drivers - temperature, precipitation and agriculture - using pollen-derived estimates of diversity. Our study is unique because it builds on 805 fossil pollen samples and 80 modern pollen samples from eight locations across the Eastern Mediterranean, including Turkey, Cyprus, Syria, Lebanon and Israel (Fig. S1). Our goal is to reconstruct the evolution of plant diversity over the

last 8000 years (from 52 to 7720 BP; Fig. 1), to compare and contrast this dynamic with the current state of diversity and to suggest potential scenarios for the future through the lens of past reconstructions. We aim to examine how human-related activities and climate change have affected regional ecosystems over a long period by analyzing past and present trends in terrestrial plant diversity.

## 2. Methods

### 2.1. Cores and chronology

Our fossil and modern pollen database comprises 16 records (8 fossil records - 805 samples; 8 modern records - 80 samples) from eight different locations across the Eastern Mediterranean/Levant region. These locations include: Bereket in Turkey (0-3500 BP; Kaniewski et al., 2007), Hala Sultan Tekke/Larnaca Salt Lake in Cyprus (500-5800 BP; Kaniewski et al., 2020), Tell Tweini (2400-4200 BP; Kaniewski et al., 2008), Jableh (0-1100 BP; Kaniewski et al., 2011) and Wadi Jarrah (0-1600 BP; Kaniewski et al., 2012) in Syria, Tyre in Lebanon (1300-7750 BP; Kaniewski et al., 2023), Tel Dan (1800-4200 BP; Kaniewski et al., 2017) and Tel Akko (50-6000 BP; Kaniewski et al., 2013) in Israel (Fig. S1). The chronology of individual cores, based on radiocarbon dates, is detailed in each article. The original chronologies (age-depth models) have been preserved in this study. The associated dating error has been averaged to  $\pm 80$  years based on all the age models.

### 2.2. Plant diversity database

*Fossil samples.* The reconstructed number of taxa ( ${}^R N_{\text{Taxa}}$ ) present in each fossil sample, reflecting the pollen/plant diversity through time, was used here as a proxy for the taxonomic richness of each site. While limitations have been mentioned (Birks and Line, 1992; Goring et al., 2013), previous studies have shown the robustness of using pollen as a proxy for reconstructing trends in plant diversity (Ivory et al., 2018; Chevalier et al., 2020; Coussin et al., 2023). A rarefaction analysis was first applied to each sequence. Rarefaction analysis provides unbiased relative estimates for the taxonomic richness and is an appropriate method for pollen samples from the same fossil record (Birks and Line, 1992). Both rarefaction and the number of taxa provide highly consistent estimates of taxonomic richness, demonstrating a strong correlation ( $0.85$ ,  $P_{\text{value}} < 10^{-3}$ ). To facilitate comparison of information on a common chronological grid, all  ${}^R N_{\text{Taxa}}$  records from Turkey to Israel were annualized using nearest-

neighbor interpolation. The eight time-series were z-score transformed to reduce inter-site variability and averaged to generate a continuous record of plant diversity covering the last 8000 years. A confidence interval (95% two-tailed confidence interval) was calculated ( $\pm 0.5$ ) and added to each data point, in addition to the dating error ( $\pm 80$  years). The continuous record of plant diversity was then interpolated to a regular 10-year increment (Fig. 1).

*Modern samples.* Modern pollen samples derive from field campaigns carried out at each site from 2007 to 2017. Sampling was combined with a field survey of the surrounding vegetation. While pollen taxa are not identified to species level, the distribution pattern reconstructed from the modern pollen dataset is consistent with field observations, suggesting a strong correlation between taxonomic richness and landscape diversity at and around each site. Modern samples were also employed in calculating a 21<sup>st</sup>-century benchmark for plant diversity, following the same methodology as applied to fossil samples. The number of taxa was calculated for each of the modern samples and the resulting data were averaged to define a score that covers the period 2007-2017. A confidence interval (95% two-tailed confidence interval) was added to this reference value (average of  $35 \pm 2.8$ ). The  $R_{N_{\text{Taxa}}}$  record was then compared and contrasted with the modern average score to transform the fossil data into anomalies (Fig. S2). The fossil and modern confidence intervals were summed and added to the anomaly curve (Fig. S2).

### 2.3. Climate database

The database for climate reconstruction derives from the same eight locations. Local helophytes, macrophytes and spores of non-vascular cryptogams were not considered in the pollen-based climate reconstruction. In addition to the secondary anthropogenic indicators (e.g. *Plantago*, *Rumex*, *Polygonum*; Behre, 1990), the cultivated species (primary anthropogenic indicators: Poaceae cerealia) were also omitted from the pollen-based climate reconstruction. The  $R_{N_{\text{Taxa}}}$  has no influence on climate reconstruction, avoiding any circular reasoning.

*Pollen-based climate reconstruction.* Pollen assemblages were used to reconstruct the palaeoclimate history of the Eastern Mediterranean. Our statistical approach presents two key caveats: (1) a fossil pollen assemblage may not have a modern analog *sensu stricto*; and (2) the climate range of a species/genus can shift in time (Cheddadi and Khater, 2016). Our

method operates under the assumption that the co-occurrence of plant taxa within an assemblage only occurs when there is a shared climate range or an overlap in the climatic preferences of the plant taxa found in that particular assemblage. Given this assumption, it is reasonable to expect that two plant species will not be found together in the same assemblage if their respective climate ranges do not intersect. We assigned the fossil pollen taxa to their closest modern counterparts. Subsequently, we calculated a weighted median value, including its standard deviations, to define the climate range encompassed by all the assigned modern species. Such an approach has been used to infer past climate variables using insects (Elias, 1997), plant fossil remains (Pross et al., 2000), mollusks (Moine et al., 2002) and ostracods (Horne, 2007). It has also been used to establish climate probability density functions from fossil pollen data (Kühl et al., 2002).

In our method (Cheddadi et al., 2017) we incorporate a "leave-one-out calculation" to account for the temporal fluctuations in pollen taxa within the fossil record for each fossil sample, one taxon is systematically excluded, and a weighted median is computed using the remaining taxa, with the pollen percentages serving as weights. This process is repeated for each taxon within a given fossil level, resulting in multiple iterations of weighted median calculations. The ultimate output is the median value derived from all these iterations. Furthermore, the standard deviations we use correspond to the median value obtained from the standard deviations generated during all of these iterations.

This additional leave-one-out approach reduces the effects of significant variations within the fossil record and helps to balance potential biases arising from the over- or under-representation of certain pollen species. The code was written using the software R and exploits the available libraries (Akima and Gebhardt, 2016), RMySQL (Ooms et al., 2016), and the statistical functions which are part of R. The modern plant database is constructed from georeferenced species data sourced from Flora Europaea (Jalas and Suominen, 1973, 1979, 1980) and GBIF (Heughebaert, 2019). Current climate data were sourced from the WORLDCLIM database (Hijmans et al., 2005). The pollen-based model used to reconstruct the climate variables has previously furnished coherent climate reconstructions (Kanievski et al., 2017, 2019, 2023).

*Temperature.* Pollen-derived mean annual temperatures for each site were subsequently transformed into anomalies ( $^{\text{R}}T_{\text{mean}}$ ) compared to present-day conditions, using the second half of the 20<sup>th</sup> century (1960-1990) as a reference point (average of  $17.1 \pm 2.8^{\circ}\text{C}$ ). All the

present-day climate data (1960-2018) were compiled during field campaigns and sourced from publicly accessible meteorological stations in the countries included in this study (mainly Burdur, Larnaca, Lattakia, Hasakah, Beirut, Haifa, Shave Ziyon, and Kefar Nahum).

*Winter precipitation.* Pollen-derived winter precipitation was also transformed into anomalies ( ${}^R\text{WP}_{\text{mm}}$ ) compared to the average score for the last 8000 years (average of  $345\pm 25$  mm). The results are presented as percentage deviations illustrating the disparity between the reference value and the reconstructed value for each sample. To facilitate comparison of information on a common chronological scale, all  ${}^R\text{T}_{\text{mean}}$  and  ${}^R\text{WP}_{\text{mm}}$  records were annualized using nearest-neighbor interpolation. The time series were averaged to generate continuous records of  ${}^R\text{T}_{\text{mean}}$  and  ${}^R\text{WP}_{\text{mm}}$  covering the last 8000 years (Fig. 1). A confidence interval (95% two-tailed confidence interval) was calculated and added to each time series ( $\pm 0.5^\circ\text{C}$  for  ${}^R\text{T}_{\text{mean}}$  and  $\pm 5\%$  for  ${}^R\text{WP}_{\text{mm}}$ ), as well as the dating error ( $\pm 80$  years). The time series were then interpolated to a regular 10-year increment.

#### 2.4. Agriculture database

Anthropogenic activities ( ${}^R\text{Agri}_{\text{cer}}$ ) exclusively encompass agricultural indicators, specifically focusing on cereals, given their long-term traceability and direct association with human influence. The threshold sizes used to discriminate cereals from other wild Poaceae (e.g. annulus thickness, pore diameter) are  $47\ \mu\text{m}$  for the grain diameter and  $11\ \mu\text{m}$  for the annulus diameter (Joly et al., 2007; Kaniewski et al., 2018). Even if *Secale* is potentially the only cereal which can be identified (prolate grain shape and eccentrically positioned pore), some cereal grains fall broadly within this range. To avoid confusion, all pollen grains attributed to cereals were included in a cereal assemblage. The cereal signal was extracted from each location. To facilitate comparison of information on a common chronological grid, all cereal records from Turkey to Israel were annualized using nearest-neighbor interpolation. The eight time series were z-score transformed to reduce inter-site variability and averaged to generate a continuous record of agriculture covering the last 8000 years. A confidence interval (95% two-tailed confidence interval) was calculated ( $\pm 0.4$ ) and added to each data point, in addition to the dating error ( $\pm 80$  years). The continuous record of agriculture was then interpolated to a regular 10-year increment (Fig. 1).

#### 2.5. Other databases



The  $R_{SST}$ s are a composite time series based on 54 records from the Mediterranean Sea (Marriner et al., 2022). This dataset was used as an independent proxy for the evolution of Eastern Mediterranean temperatures during the last 8000 years. The  $\delta^{18}O$  scores derive from Jeita Cave (Lebanon; Cheng et al., 2015) and were also used as an independent proxy for precipitation. Jeita Cave was selected as a model due to its geographical position at the heart of the Levantine region (Cheng et al., 2015).

## 2.6. Statistical analyses

Statistical analyses were performed using XL-Stat<sup>2019</sup>, R version 3.6.3 (R Core Team, 2020) and the software package PAST 4.12 (Hammer and Harper, 2006).

$R_{N_{Taxa}}$  versus  $R_{T_{mean}}$ . The link between  $R_{N_{Taxa}}$  and  $R_{T_{mean}}$  for the last 8000 years was tested, ranking the  $R_{T_{mean}}$  values in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores. Because we focused on trends,  $R_{N_{Taxa}}$  and  $R_{T_{mean}}$  were smoothed using a moving average function (30-year) and the results are shown with confidence intervals ( $R_{N_{Taxa}}$  and  $R_{T_{mean}}$ , 95% two-tailed confidence intervals). This first step is termed  $R_{N_{Taxa}}$  raw and is displayed as data points (Fig. 2a) and continuous lines (Fig. 2b). The long-term trend was calculated using a polynomial model (termed  $PM^1$ ; order 5,  $P_{value} < 10^{-3}$ ) with a  $P_{value}$  based on a F test - two-tailed, with no adjustment. The tipping point corresponds to the highest score of  $PM^1$  (with the associated confidence intervals). We then added boxplots to probe the evolution of plant diversity every 0.5°C.

For potential future scenarios, we used the  $PM^1$  equation to project a possible evolution of plant diversity, based on an increasing gradient of  $R_{T_{mean}}$  as proposed by the IPCC (2021, 2022a). Confidence intervals ( $R_{N_{Taxa}}$  and  $R_{T_{mean}}$ , 95% two-tailed confidence intervals) and the different SSP scenarios were added to the projection (IPCC, 2021; Fig. 2b).

$R_{N_{Taxa}}$  versus  $R_{WP_{mm}}$ . The link between  $R_{N_{Taxa}}$  and  $R_{WP_{mm}}$  for the last 8000 years was tested, ranking the  $R_{WP_{mm}}$  values in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores. As we focused on trends,  $R_{N_{Taxa}}$  and  $R_{WP_{mm}}$  were smoothed using a moving average function (30-year) and the results are shown with confidence intervals ( $R_{N_{Taxa}}$  and  $R_{WP_{mm}}$ , 95% two-tailed confidence intervals). This first step is termed  $R_{N_{Taxa}}$  raw and is displayed as data points (Fig. 3a) and continuous lines (Fig. 3b). The long-term trend was calculated using a polynomial model (termed  $PM^2$ ; order 5,  $P_{value} < 10^{-3}$ ) with a  $P_{value}$  based on a F test - two-tailed, with no

adjustment. The tipping point corresponds to the highest score of  $PM^2$  (with the associated confidence intervals). We then added boxplots to probe the evolution of plant diversity at 5% increments.

To explore potential future scenarios, we used the  $PM^2$  equation to suggest the future trend of plant diversity under a decreasing gradient of precipitation (Fig. 3b). The rate of precipitation decline was calculated between 2000-2010 and 2010-2020 based on local public weather stations (-1 mm per year) and then extrapolated up to 2100. Confidence interval bands ( $R_{N_{Taxa}}$  and  $R_{WP_{mm}}$ , 95% two-tailed confidence intervals) were added to the projection (Fig. 3b).

*$R_{N_{Taxa}}$  versus  $R_{AgriCer}$ .* The link between  $R_{N_{Taxa}}$  and  $R_{AgriCer}$  for the last 8000 years was tested, ranking the  $R_{AgriCer}$  values in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores. As we focused on trends,  $R_{N_{Taxa}}$  and  $R_{AgriCer}$  were smoothed using a moving average function (30-year) and the outcomes are shown with confidence intervals ( $R_{N_{Taxa}}$  and agriculture, 95% two-tailed confidence intervals). This first step is termed  $R_{N_{Taxa}}$  raw and is displayed as data points (Fig. 4a) and continuous lines (Fig. 4b). The long-term trend was calculated using a polynomial model (termed  $PM^3$ ; order 5,  $P_{value} < 10^{-3}$ ) with a  $P_{value}$  based on a F test - two-tailed, with no adjustment. The tipping point corresponds to the highest score of  $PM^3$  (with the associated confidence intervals). We then added boxplots to probe the evolution of plant diversity every 0.5.

To investigate potential future scenarios, we employed the  $PM^3$  equation to suggest the future trajectory of plant diversity as agriculture intensifies along an increasing gradient (Fig. 4b). Agriculture during the industrial era was calculated for the period 1900-1950 based on fossil samples and for the period 2007-2017 using modern samples. Confidence interval bands ( $R_{N_{Taxa}}$  and  $R_{AgriCer}$ ; 95% two-tailed confidence intervals) were added to the projection (Fig. 4b).

*$R_{N_{Taxa}}$  versus  $R_{SSTs}$ .* The link between  $R_{N_{Taxa}}$  and Mediterranean  $R_{SSTs}$  for the last 8000 years was tested, ranking the  $R_{SST}$  values in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores.  $R_{N_{Taxa}}$  and  $R_{SSTs}$  were smoothed using a moving average function (30-year) and the results are shown with confidence intervals ( $R_{N_{Taxa}}$  and  $R_{SSTs}$ , 95% two-tailed confidence intervals). They are displayed as data points (Fig. S3a). The long-term trend was calculated

using a polynomial model (termed PM<sup>4</sup>; order 5,  $P_{value} < 10^{-3}$ ) with a  $P_{value}$  based on a F test - two-tailed, with no adjustment. The tipping point corresponds to the highest score of PM<sup>4</sup> (with the associated confidence intervals). We then added boxplots to assess the evolution of plant diversity every 0.1°C. The link between  $R_{T_{mean}}$  and  $R_{SSTs}$  was tested using a linear model (Fig. S3b).

*$R_{N_{Taxa}}$  versus  $\delta^{18}O$  scores - Jeita Cave.* The link between  $R_{N_{Taxa}}$  and  $\delta^{18}O$  scores for the last 8000 years was tested, ranking the  $\delta^{18}O$  values in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores.  $R_{N_{Taxa}}$  and  $\delta^{18}O$  scores were smoothed using a moving average function (30-year) and the outcomes are shown with confidence intervals ( $R_{N_{Taxa}}$ , 95% two-tailed confidence interval). This step is displayed as data points (Fig. S4a). The long-term trend was calculated using a polynomial model (termed PM<sup>5</sup>; order 5,  $P_{value} < 10^{-3}$ ) with a  $P_{value}$  based on a F test - two-tailed, with no adjustment. The tipping point corresponds to the highest score of PM<sup>5</sup> (with the associated confidence interval). We then added boxplots to probe the evolution of plant diversity every 0.15 ‰. The link between  $R_{WP_{mm}}$  and  $\delta^{18}O$  scores was tested using a linear model (Fig. S4b).

*Three drivers.* A PCA was subsequently performed, using  $R_{T_{mean}}$ ,  $R_{WP_{mm}}$  and  $R_{Agri_{Cer}}$  as a matrix (Fig. S5a). To ensure consistency and comparability, we initially subjected the time series data to z-score transformation before initiating any analytical procedures. The link between  $R_{N_{Taxa}}$  and the PCA-Axis 1 was tested, ranking the PCA-Axis 1 scores in ascending order and retaining the associated  $R_{N_{Taxa}}$  scores. As we focused on trends, PCA-Axis 1 and  $R_{N_{Taxa}}$  scores were smoothed using moving average functions (30-year and 200-year; Fig. S5a-b). The outcomes are shown with a 95% two-tailed confidence interval band. Linear models were then applied to test the relationship between  $R_{N_{Taxa}}$  and the combined three drivers (Fig. S5a-b).

## 2.7. Data availability

The Excel file contains all of the data used in this study.

## 3. Results

### 3.1. Pollen-based vegetation reconstruction of plant diversity

To evaluate historical and current trends in plant diversity, we used pollen-based vegetation reconstructions, a reliable proxy that can capture changes in vegetation diversity and taxonomic richness over time (Fernández-Llamazares et al., 2014; Matthias et al., 2015; Connor et al., 2021). Studies have demonstrated that the diversity detected in pollen samples is comparable to that found in the biomes from which they were collected, indicating a strong correlation between taxonomic richness and landscape diversity (Ivory et al., 2018). We here selected the number of taxa (termed reconstructed number of taxa -  ${}^R\text{N}_{\text{Taxa}}$ ) per sample as a proxy, which is supported by the literature (Ivory et al., 2018; Chevalier et al., 2020; Coussin et al., 2023), to generate an 8000-year reconstruction of plant diversity (Fig. 1). The outcome, shown as z-scores, depicts the average value of plant diversity resulting from all the time series (from Turkey to Israel). We subsequently transformed past mean annual temperatures into anomalies (termed reconstructed mean annual temperature anomalies -  ${}^R\text{T}_{\text{mean}}$ ) and past winter precipitation into deviations (termed reconstructed winter precipitation deviations -  ${}^R\text{WP}_{\text{mm}}$ ), respectively using the second half of the 20<sup>th</sup> century (1960-1990; average of  $17.1\pm 2.8^\circ\text{C}$ ) and the average score for the last 8000 years (average of  $345\pm 25$  mm) as reference points. The proxy for agriculture (termed reconstructed agriculture-cereals -  ${}^R\text{Agri}_{\text{Cer}}$ ) derives from a z-score signal that was extracted from each location and averaged to generate a single time series.

### 3.2. Long-term trends in plant diversity

The  ${}^R\text{N}_{\text{Taxa}}$ ,  ${}^R\text{T}_{\text{mean}}$ ,  ${}^R\text{WP}_{\text{mm}}$  and  ${}^R\text{Agri}_{\text{Cer}}$  time series have been plotted on a chronological scale (Fig. 1) to estimate the long-term trends in plant diversity, annual temperatures, winter precipitation and agriculture. The  ${}^R\text{N}_{\text{Taxa}}$  time series shows that plant diversity was important during the period  $6550\text{-}5750\pm 80$  BP, and that since  $5750\pm 80$  BP, there is a gradual decrease in Eastern Mediterranean plant diversity, when considering the polynomial model ( $R^2 = 0.62$ ,  $P_{\text{value}} < 10^{-3}$ ). The lowest values occur during the period  $1550\text{-}1300\pm 80$  BP, centered on the Late Antique Little Ice Age (Büntgen et al., 2016), and the period  $110\text{-}500\pm 80$  BP, during the pre-industrial Little Ice Age (Matthews and Briffa, 2004). When the  ${}^R\text{N}_{\text{Taxa}}$  time series is converted into anomalies (using the 2007-2017 score as the reference value; Fig. S2), only the period  $1500\text{-}1300\pm 80$  BP (as well as isolated points around  $1150\pm 80$  BP and  $300\pm 80$  BP) is similar to the present-day value, suggesting that present plant diversity is significantly lower when compared to the plant diversity observed over the past 8000 years. To understand the

present status of biological diversity, we compared and contrasted the evolution of plant diversity in conjunction with fluctuations in three key factors – temperature, precipitation, and agriculture – over the course of the past 8000 years.

### 3.3. Plant diversity versus temperature

When  $R_{N_{\text{Taxa}}}$  in the Eastern Mediterranean is plotted against  $R_{T_{\text{mean}}}$  (Fig. 2a), the above-average values (potential tolerance range) fall between  $-0.1 \pm 0.5^\circ\text{C}$  and  $2.5 \pm 0.5^\circ\text{C}$ , but with a tipping point at  $1.33 \pm 0.5^\circ\text{C}$  when considering the polynomial model ( $\text{PM}^1$ :  $R^2 = 0.8$ ,  $P_{\text{value}} < 10^{-3}$ ). This long-term view suggests decreasing  $R_{N_{\text{Taxa}}}$  scores from a  $R_{T_{\text{mean}}}$  of  $1.33 \pm 0.5^\circ\text{C}$  (negative trend), a range that nonetheless already includes the SSP1-1.9 scenario [low greenhouse gas (GHG) emissions; IPCC] (IPCC, 2021) which stabilizes modern/future mean average temperatures at an increase of  $1.5^\circ\text{C}$ , a threshold that the Eastern Mediterranean/Middle East region surpassed in 2019 (Zittis et al., 2022). This implies that, as of 2019, the Eastern Mediterranean region has either transgressed its tipping point at  $1.33^\circ\text{C}$  or is close to reaching this critical threshold, particularly when considering the temperature range associated with the tipping point ( $1.33 \pm 0.5^\circ\text{C}$ ). When past plant diversity is plotted against an independent proxy, Mediterranean Sea Surface Temperatures (termed reconstructed Sea Surface Temperature anomalies -  $R_{\text{SSTs}}$ ; Marriner et al., 2022), the association between  $R_{T_{\text{mean}}}$  and  $R_{N_{\text{Taxa}}}$  is further strengthened. We defined a tipping point of  $0.42 \pm 0.16^\circ\text{C}$  when considering  $R_{N_{\text{Taxa}}}$  versus  $R_{\text{SSTs}}$  (Fig. S3a). By analyzing  $R_{T_{\text{mean}}}$  and  $R_{\text{SSTs}}$  using a linear model ( $R^2 = 0.80$ ,  $P_{\text{value}} < 10^{-3}$ ), we found that the  $1.33 \pm 0.5^\circ\text{C}$  increase in  $R_{T_{\text{mean}}}$  is correlated with a  $0.42 \pm 0.16^\circ\text{C}$  increase in  $R_{\text{SSTs}}$  (Fig. S3b). This strong correlation supports the idea that climate variations have played a significant role in shaping plant diversity trends, manifesting both positive and negative impacts. To project the potential impact of rising mean average temperatures on plant diversity, we employed the  $\text{PM}^1$  equation (Fig. 2b) and examined various SSP scenarios for the year 2100 (IPCC, 2021). If scenarios SSP1-1.9 or SSP1-2.6 are followed (low GHG emissions scenario; IPCC, 2021), there is a potential for moderating plant-diversity loss in contrast to the current trajectory. Our analysis indicates that under scenario SSP2-4.5 (intermediate GHG emissions scenario; IPCC, 2021), the projected loss of plant diversity (as shown in Fig. 2b) would be significant, potentially leading to a marked shift in the composition of Mediterranean flora.

### 3.4. Plant diversity versus precipitation

Winter was used as the reference season because maximum rainfall occurs in December to February in both the northern and southern Levant (two-thirds of the annual rainfall; Baruch et al., 2006; Zeleňáková et al., 2022). When examining the relationship between  $R_{\text{Taxa}}$  and  $R_{\text{WP}_{\text{mm}}}$  (Fig. 3a), we found that the highest levels of past diversity were associated with precipitation levels between  $-2\pm 5\%$  and  $20\pm 5\%$  ( $338\pm 25$  and  $414\pm 25$  mm). Our polynomial model ( $\text{PM}^2$ ) shows a tipping point at  $9\pm 5\%$  ( $359\text{--}393$  mm;  $R^2 = 0.74$ ,  $P_{\text{value}} < 10^{-3}$ ), indicating that deviations from this threshold could have a significant impact on Eastern Mediterranean plant communities. Our analysis reveals that the current score for winter precipitation in the Eastern Mediterranean, spanning from 2000-2010 and 2010-2020, stands respectively at around  $-8.1\pm 5\%$  ( $317\pm 25$  mm) and  $-11\pm 5\%$  ( $307\pm 25$  mm) based on weather stations. This value is approximately  $70\pm 25$  mm lower than the tipping point identified by  $\text{PM}^2$ , which suggests that the observed decline in precipitation levels in the region (Zeleňáková et al., 2022) has already had a significant impact on local plant diversity (Fig. 3b).  $\text{PM}^2$  was further used to analyze the effect of a continuous decline in precipitation on plant diversity in the near future (Fig. 3b). The average rate of decreasing precipitation between 2000-2010 and 2010-2020 is 1 mm per year, suggesting that, if this rate remains constant, winter precipitation will be approximately  $277\pm 25$  mm by 2040-2050 and  $227\pm 25$  mm in 2090-2100 (Fig. 3b). Our model suggests that the impact on plant diversity is likely to be substantial. When  $R_{\text{Taxa}}$  is further plotted against an independent proxy for precipitation,  $\delta^{18}\text{O}$  scores from Jeita Cave (Lebanon; Cheng et al., 2015), the connection between plant diversity and rainfall becomes even more robust. We defined a tipping point of  $-5.56\text{‰}$  when considering  $R_{\text{Taxa}}$  versus  $\delta^{18}\text{O}$  (Fig. S4a). By analyzing  $R_{\text{WP}_{\text{mm}}}$  and  $\delta^{18}\text{O}$  using a linear model ( $R^2 = 0.85$ ,  $P_{\text{value}} < 10^{-3}$ ), we found that the  $9\pm 5\%$  increase in  $R_{\text{WP}_{\text{mm}}}$  is correlated with a  $-5.56\text{‰}$  score in  $\delta^{18}\text{O}$  (Fig. S4b). Winter precipitation is thus key to explaining variations in plant diversity. The apparently lower sensitivity of plant diversity to precipitation as compared to temperature could be attributed to several factors, including plant plasticity (Midolo and Wellstein, 2020). Additionally, precipitation affects plant growth and survival through a wide range of ecological processes that are more complex than those governed by temperature alone. These processes include the seasonal distribution of rainfall, hydrology, soil depth and type, and access to groundwater (Moles et al., 2014), ultimately making precipitation a more critical factor in determining plant diversity.

### 3.5. Plant diversity versus agriculture

$R_{\text{AgriCer}}$  (cereal production) was selected as a marker of human impact on plant diversity as these activities can be traced and quantified over a long period of time (Fig. 4a-b). Higher scores indicate greater levels of pressure exerted on the environment. When  $R_{\text{NTaxa}}$  is plotted against  $R_{\text{AgriCer}}$  (Fig. 4a), most of the above-average values (tolerance range) fall between  $-1.4 \pm 0.4$  and  $-0.5 \pm 0.4$  (low to medium pressures), with a tipping point at  $-1.05 \pm 0.4$  according to the polynomial model (PM<sup>3</sup>:  $R^2 = 0.58$ ,  $P_{\text{value}} < 10^{-3}$ ). The current score (2007-2017; based on modern samples) is  $2.1 \pm 0.4$  (high pressures), suggesting that the maximum stress on plant diversity has occurred since the onset of the 21<sup>st</sup> century. When we contrast the present score with the 1900-1950 value of  $1.5 \pm 0.4$  (derived from the most recent fossil samples), it becomes evident that the 20<sup>th</sup> century was a period of relatively stable and moderate plant diversity conservation. However, the score for the period 2000-2020 suggests that we are now approaching a value dangerously near the threshold defined by the  $R_{\text{AgriCer}}$  before experiencing substantial diversity loss (Fig. 4b). The projected increase of 90 million inhabitants in the Mediterranean region over the next 30 years (2020-2050), bringing the total population to 611 million, with two-thirds concentrated on the southern and eastern seaboard, is expected to impose substantial stress on the environment as it struggles to provide for this growing population (Ambrosetti, 2020). This mounting pressure on vegetation will inevitably intensify the already significant loss of plant diversity (Fig. 4b).

### 3.6. Plant diversity versus the three drivers

We subsequently performed a principal component analysis (PCA) using  $R_{\text{Tmean}}$ ,  $R_{\text{WPmm}}$  and  $R_{\text{AgriCer}}$  (using z-scores for all the time series). PCA-Axis 1, which loads the maximum variability (65.1%), was used as a proxy combining the three drivers having a significant influence on plant diversity. We furthermore ran linear models to assess the link between changes in plant diversity and the PCA-Axis 1 scores (Fig. S5a-b). Our analysis revealed a linear relationship between plant diversity and the cumulated pressures of the three primary drivers, both for short-term ( $R^2 = 0.76$ ,  $P_{\text{value}} < 10^{-3}$ ; Fig. S5a) and long-term trends ( $R^2 = 0.89$ ,  $P_{\text{value}} < 10^{-3}$ ; Fig. S5b). While isolating the three drivers (Figs. 2-4) provides insights into their individual contributions, it falls short of capturing the intricate interplay of multiple pressures and processes that collectively shape the observed trend. Previous studies have shown that plant diversity is influenced by climate and land use (Higgins, 2007), but the combined effect of each

threat has the most significant impact (Mantyka-Pringle et al., 2011). Our study confirms that plant diversity is threatened not by a single factor but by a combination of interacting variables.

#### **4. Discussion**

Our investigation suggests that, during the last 8000 years, there were adjustments in plant diversity in response to the gradual evolution of environmental stressors, followed by the emergence of human pressures. According to several authors (Santamaría and Méndez, 2012; Urban et al., 2012; Garcia-López and Allué, 2013), current human activities trigger fast evolutionary responses which result in the establishment of new communities and co-evolutionary networks for which there are no past analogues. The plurisecular evolution of plant diversity in the Eastern Mediterranean is consistent with these findings regarding agriculture (Fig. 4b) and winter precipitation (Fig. 3b) where fossil analogues will soon be lacking. Regarding  $R_{T_{mean}}$ , our analysis suggests that the Eastern Mediterranean may have experienced warmer phases over the last 8000 years. However, it is important to note that all the drivers of plant diversity, including climate and land use, act in concert and mutually reinforce each other. Therefore, it is likely that since the onset of the Anthropocene, rising temperatures have added to and amplified the impact of other human activities, such as changes in land use, as well as droughts, leading to the observed decline in plant diversity.

The preservation of plant diversity and the ecosystem services it provides are inherently linked to both climate change (Sintayehu, 2018; Suggitt et al., 2019) and the extent and direction of anthropogenic pressures/agriculture (Ellis, 2019). Since the onset of the Industrial Revolution, climate change has laid the foundation for a paradigm shift, leading to significant threats to plant diversity. The impacts of these threats are expected to increase as climate change accelerates, and human activities continue to artificialize the natural environment through activities such as urbanization and industrial-scale agriculture. With the benefit of 8000 years of historical perspective, it is evident that the current state of plant diversity in the Eastern Mediterranean has already exceeded its sustainable limits. The current situation is unprecedented in the last 8000 years and highlights the vulnerability of the plant communities that have thrived in the region, from Turkey to Israel. There is a significant risk that this plant diversity may experience a sharp decline and be replaced by species that are better suited to the unique conditions resulting from both climate change and human activities.



## 5. Conclusion

Plant diversity is a major concern regarding current and future environmental changes in the Mediterranean. Our analysis, focused on the eastern part of the Mediterranean basin, suggests that over the last 8000 years, a tipping point of plant diversity can be established for three key parameters, temperatures ( $1.33\pm 0.5^{\circ}\text{C}$ ), precipitation ( $376\pm 17$  mm) and anthropogenic activity ( $-1.05\pm 0.4$  - low to medium pressures). Exceeding this threshold (either positive or negative anomalies) leads to a decline in plant diversity, with the magnitude of the decline varying depending on the specific parameter being considered. Our study primarily underscores the multifaceted nature of plant diversity threats, suggesting that it is not a consequence of a singular factor, but rather a complex interplay of synergistically interacting variables. In the near future, the Eastern Mediterranean's plant diversity is likely to undergo a significant shift, with African species, better adapted to dry and arid conditions, gaining a foothold and displacing native plants that have dominated the region's landscapes for thousands of years.

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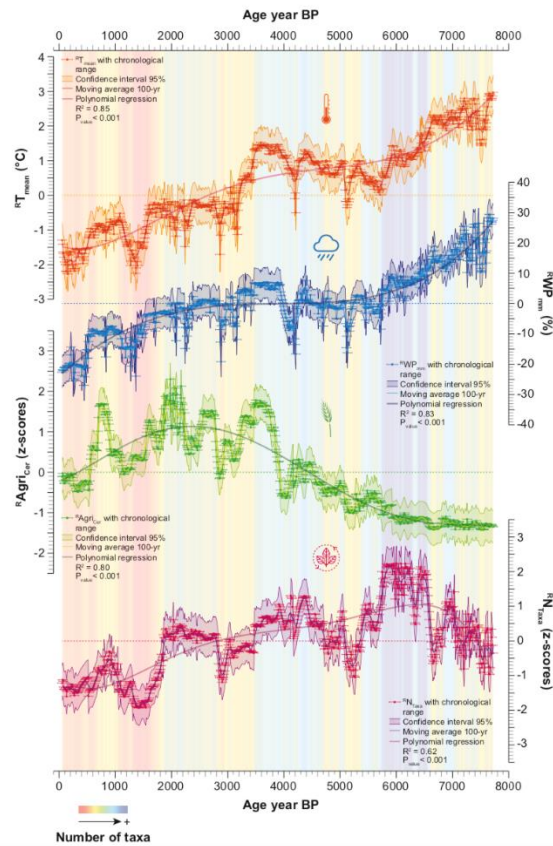
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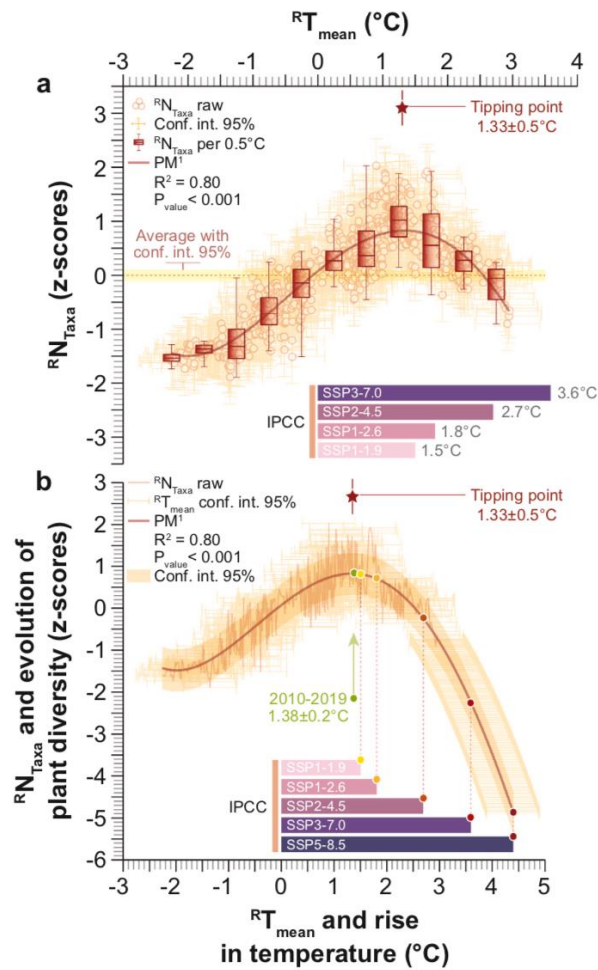
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**Competing Interest Statement:** The authors declare no competing interests.

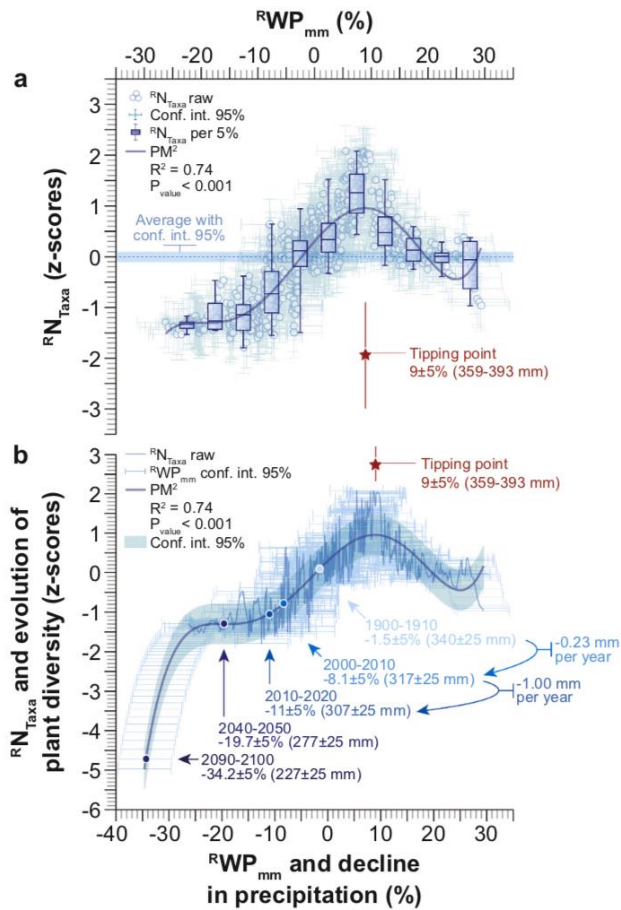
## Figures



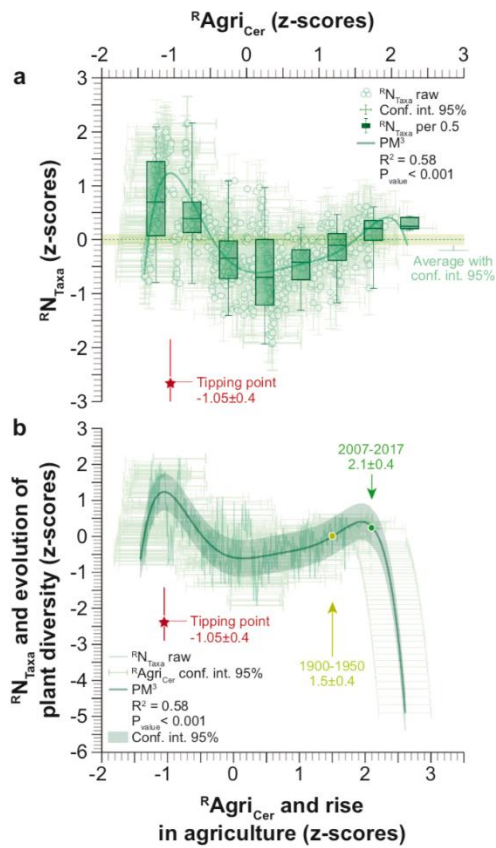
**Figure 1.** Temperature, winter precipitation, agriculture and plant diversity during the last 8000 years.  $R^T_{mean}$  scores are shown as anomalies (°C),  $R^{WP}_{mm}$  as percentage deviations (%),  $R^{Agri}_{Cer}$  as z-scores and  $R^{N_{Taxa}}$  as z-scores. A 95% confidence interval and the chronological range were added for each time series. The long-term trend is shown as a 100-year moving average and polynomial model for each time series. The colored background signifies fluctuations in plant diversity, transitioning from red, denoting low diversity, to blue, indicating high diversity. The chronological scale is expressed in BP (before 1950).



**Figure 2.** Evolution of plant diversity according to an increasing temperature gradient. **(a)**  $R_{T_{mean}}$  ( $^{\circ}C$ ) are ranked in ascending order, retaining the associated  $RN_{Taxa}$  scores (shown as data points, with 95% confidence intervals). The average value is highlighted by a dotted line, accompanied by a 95% confidence interval. The long-term trend is represented using a polynomial model ( $PM^1$ , order 5,  $P_{value} < 10^{-3}$ ), with the tipping point corresponding to the highest score on the curve (red star). The associated boxplots illustrate the evolution of  $RN_{Taxa}$  every  $0.5^{\circ}C$ . **(b)** Evolution of plant diversity depending on the current-future rise in temperatures - based on the  $PM^1$  equation (with 95% confidence interval bands). The  $RN_{Taxa}$  scores are shown as a continuous line. The different Shared Socioeconomic Pathways (SSPs) were added to the projection (IPCC, 2021, 2022a).



**Figure 3.** Evolution of plant diversity according to a decreasing gradient of winter precipitation. (a)  $R^{WP}_{mm}$  is ranked in ascending order, retaining the associated  $R^N_{Taxa}$  scores (shown as data points, with 95% confidence interval bands). The average value is highlighted by a dotted line (with a 95% confidence interval). The long-term trend is shown using a polynomial model (PM<sup>2</sup>, order 5,  $P_{value} < 10^{-3}$ ), with the tipping point corresponding to the highest score on the curve (red star). The associated boxplots illustrate the evolution of plant diversity at 5% increments. (b) Evolution of plant diversity depending on the current-future decline in precipitation - based on the PM<sup>2</sup> equation (with 95% confidence interval bands). The  $R^N_{Taxa}$  scores are shown as a continuous line. The rate of precipitation decline was calculated between 2000-2010 and 2010-2020 and extrapolated up to 2100.



**Figure 4.** Evolution of plant diversity in relation to an ascending gradient of agriculture. (a)  $R^{Agri}_{Cer}$  is ranked in ascending order, retaining the associated  $R^N_{Taxa}$  scores (shown as dots, with 95% confidence interval bands). The average value is shown as a dotted line, accompanied by a 95% confidence interval. The long-term trend is depicted by a polynomial model ( $PM^3$ , order 5,  $P_{value} < 10^{-3}$ ), with the tipping point corresponding to the highest score on the curve (red star). The associated boxplots illustrate the evolution of plant diversity every 0.5 increment. (b) Evolution of plant diversity depending on the current-future rise in agriculture - based on the  $PM^3$  equation (with 95% confidence interval bands). The  $R^N_{Taxa}$  scores are shown as a continuous line. Agriculture scores were calculated for the periods 1900-1950 and 2007-2017.