

Tools and approaches to addressing the climate-humans nexus during the Holocene

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Tools and Approaches to Addressing the Climate-Humans Nexus during the Holocene

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Abstract

The impact of humans on climate and landscape is obvious today when anthropogenic climate change impacts are being felt around the world and more than 10% of the land surface is intensively managed. However, transformations of natural ecosystems by humans began with the shift from hunting and gathering to cultivation during the Mesolithic and Neolithic periods. There have also been substantial changes in climate during the Holocene, giving rise to natural changes in vegetation cover and fire regimes. It is important to quantify the impact of natural and anthropogenic influences on landscapes at a regional scale, and understand how climate-induced changes affected the resources available to people and hence the expansion of human populations, to provide a firm foundation for interpreting human development in the past and for predicting human-environment interactions in the future. Several recent developments make it possible to address these issues more systematically. New statistical tools have been developed that provide independent and robust quantitative reconstructions of past changes in climate, vegetation and fire regimes through the Holocene. These reconstructions can be compared with evidence for population growth and/or agricultural practices at a regional scale to isolate human and natural impacts on ecosystems and disturbance regimes. Process-based modelling tools, including eco-evolutionary optimality models of gross primary production and of specific crop types, can be used to disentangle the roles of climate, climate variability, changes in atmospheric CO₂ levels, and agricultural practices on agricultural yields through time. Transient climate model simulations can be used to examine the response of regional climates to changes in external forcing through time and also the interaction between long-term trends in climate, changes in climate modes and unforced climate variability. Together, these tools can be used to foster a better understanding of the climate-human nexus during the Holocene.

Introduction

The influence of human activities on the natural world today is obvious: anthropogenic greenhouse gas emissions have modified atmospheric composition with direct impacts on the climate system (IPCC 2021), while human-induced changes in land use have indirect consequences for climate (IPCC 2021) and affect biodiversity, ecosystem functioning and

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the natural resource base (IPCC 2022). Almost half of the ice-free land surface is under human use today, and much of the rest of the world is influenced to some extent by human activities (Foley *et al.* 2005; Ellis and Ramankutty 2008; Ellis *et al.* 2013). The magnitude of the impact of human activities on landscapes and climate before the industrial revolution is still a matter of debate (Ruddiman 2003; Joos *et al.* 2004; Kaplan *et al.* 2011; Singarayer *et al.* 2011; Mitchell *et al.* 2013; Stocker *et al.* 2017; Harrison *et al.* 2020). However, the modification of natural ecosystems by humans began with the time-transgressive shift from hunting and gathering to cultivation during the Mesolithic to Neolithic transition (Mazoyer and Roudart 2006; Zohary, Hopf and Weiss 2012; Tauger 2013; Maezumi *et al.* 2018) and the later Holocene is marked by increasing evidence of human impact as a result of the spread of agriculture from the Middle East across Europe during the Neolithic.

As the evidence of the impact of recent climate changes on food security and livelihoods (Rosenzweig *et al.* 2014; Hasegawa *et al.* 2018; Lesk *et al.* 2021; IPCC 2022) shows, there is a two-way relationship between humans and climate: climate change and climate variability have a profound effect on resource availability and on human well-being. The Holocene was characterised by large changes in climate, caused by latitudinal and seasonal shifts in incoming solar radiation (insolation) caused by changes in the Earth's orbit (Crucifix *et al.* 2002; Wanner *et al.* 2008). Interactions (or feedbacks) with other elements of the climate system also resulted in more abrupt shifts in climate with multi-centennial duration: for example, changes in oceanic circulation associated with meltwater discharge into the North Atlantic gave rise to an abrupt and quasi-global event around 8.2 ka (Alley *et al.* 1997; Morrill *et al.* 2013; Matero *et al.* 2017; Parker and Harrison 2022). Externally forced changes in climate are also associated with changes in climate modes, such as the El Niño Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO), which result in substantial changes in regional climates on decadal to multi-decadal timescales (e.g. Brown *et al.* 2020; Hernández *et al.* 2020; Carré *et al.* 2021; Parker and Harrison 2022). Regionally coherent climate changes during the Holocene were sufficiently large to have had a substantial impact on the natural landscape and on the resources available to people. Indeed, the impact of even comparatively small changes in climate could have had a non-negligible effect on human populations with a relatively low technological base at the beginning of the Neolithic.

The attribution of cause and effect can be difficult because of the complex and two-way interactions between climate, vegetation, disturbance and humans. Climate change has multiple impacts on natural ecosystems, causing changes in vegetation productivity (Zhu *et al.* 2016; Cai and Prentice 2020; Piao *et al.* 2020) and, through competition, on species distributions (Parmesan and Yohe 2003; Parmesan 2006; VanDerWal *et al.* 2013), and to changes in vegetation type when the climate change is sufficiently large (Huntley and Webb 1989; Prentice *et al.* 2000; Harrison and Sanchez Goñi 2010). Climate change also impacts vegetation disturbance, for example through wildfires (Krawchuk *et al.* 2009; Daniau *et al.* 2012; Marlon *et al.* 2013) and the incidence of windthrow events (e.g. Gregow, Laaksonen and Alper 2017; Seidl *et al.* 2017). Vegetation disturbance has feedbacks to climate, through for example the greenhouse gas emissions associated with wildfires or change in land-surface albedo associated with large-scale windthrow events. Climate changes also have direct effects on human well-being and productivity (Sarofim *et al.* 2016; Doherty, Heal and O'Connor 2017; Rocque *et al.* 2021), as well as impacting the suitability for different crops and other farming practices (Rosenzweig and Parry 1994; Zhao *et al.* 2017). However, human activities that modify the

landscape also affect the incidence of vegetation disturbance, including the extent and the severity of wildfires (Bowman *et al.* 2011; Andela *et al.* 2017). These impacts are not the same everywhere. The impact of human activities on wildfire, for example, depends on the kind of vegetation and whether it is fire-prone or fire-adapted (Harrison *et al.* 2021), as illustrated in model experiments which compare the incidence, size and intensity of wildfire under modern climate conditions depending on the presence and absence of human influences (Fig. 1). This level of complexity has meant that it has often proved difficult to determine the relationship between climate and human activities during the Holocene and many existing interpretations are based on apparent correlations and assumptions about cause and effect. More robust tools are needed to disentangle changes in the climate-human nexus unambiguously.

In this paper, we will discuss some of the tools now available to address this challenge. Specifically, we will examine tools to reconstruct different elements (climate, vegetation, fire, people) independently and statistical and process-based modelling approaches that can be used for hypothesis testing. We will provide a case study focusing on Iberia to show how these tools can be used to address specific questions about climate-human interactions. Finally, we will discuss ways in which the palaeoenvironmental and archaeological communities could work together more effectively to understand the changing nature of human-climate interactions during the Holocene.

Reconstruction tools

Many types of palaeoenvironmental evidence have been used to make qualitative inferences about changes in regional climate during the Holocene. Pollen records of vegetation changes between more open vegetation types and forests, for example, have been interpreted as indicating shifts from drier to wetter, or colder to warmer, conditions (e.g. Harrison and Sanchez Goñi 2010). Similarly, records of changes in lake levels have been interpreted as indicating changes in the moisture balance over the lake and its catchment (Cheddadi *et al.* 1997; De Cort *et al.* 2021). Geomorphic evidence, including the presence of loess, dunes or fluvial deposits also indicate changing climatic conditions (Macklin, Lewin and Woodward 2012; Lehmkuhl *et al.* 2021). While qualitative interpretations can be useful, many of these indicators are influenced by multiple climate variables making it hard to disentangle the specific nature of the change in climate.

Climate reconstructions

Quantitative reconstructions of specific climate variables have been made from several types of biological records, including pollen, diatoms, chironomids and beetles (e.g. Fritz *et al.* 1991; Elias 1997; Lotter *et al.* 1997; Mauri *et al.* 2015; Tarrats *et al.* 2018; Sinopoli *et al.* 2019; Liu *et al.* 2021), based on the idea that individual taxa are subject to bioclimatic limits on their distribution (Woodward 1987; Harrison *et al.* 2009). There are two basic approaches: statistical methods or inversion of process-based models. While model inversion (e.g. Wu *et al.* 2007; Garreta *et al.* 2010; Izumi and Bartlein 2016) may seem to be the ideal way to take account of all the factors that could influence species distribution, including competition and the role of changing CO₂ on physiological processes in the case of plants, the results are highly contingent on the quality of the model used (Chevalier *et al.* 2020). The tendency to use relatively simple models because of the additional uncertainties involved in inverting complex models means the outcomes have not been very satisfactory. Statistical methods

have been more widely used to reconstruct past climates and multiple statistical approaches have been developed. These can broadly be divided into regression-based techniques such as inverse regression (Huntley and Prentice 1988) or weighted averaging partial least squares regression (ter Braak and Juggins 1993), artificial neural networks (Peyron *et al.* 1998), modern analogues (Overpeck, Webb and Prentice 1985), and response surfaces (Bartlein, Prentice and Webb 1986). Bartlein *et al.* (2011) have summarised the advantages and disadvantages of these various techniques in the context of pollen-based reconstructions.

All statistical techniques are necessarily based on modern relationships between taxon distribution and climate variables, and thus they share a number of problems. The first is the need to identify the appropriate climate variable (or variables) that control the distribution of the organisms. Many pollen-based reconstructions, for example, provide estimates of mean annual temperature which is not related to any mechanism that controls plant growth. Seasonal temperature reconstructions (January or July temperature, or winter and summer temperatures defined as December-January-February and June-July-August) provide a closer approximation to the mechanisms controlling plant growth — the necessity to avoid frost damage and the requirement for energy for growth — but nevertheless they are approximations and the mean temperature of the coldest month (MTCO) and the accumulated temperature sum during the growing season (growing degree days, GDD) are more physically appropriate measures to reconstruct (Woodward 1987; Harrison *et al.* 2009). Variable selection is even more problematic in reconstructions based on aquatic organisms such as chironomids, which are usually used to reconstruct summer air temperature (e.g. Heiri *et al.* 2003; Tarrats *et al.* 2018) although they are known to be influenced by water temperature and the depth and stability of the lake thermocline (Luoto *et al.* 2014; Matthews-Bird *et al.* 2016).

A final issue that affects statistically based climate reconstructions is whether the modern day can provide realistic analogues for the past. The generic example of this is the more seasonally contrasted climates of the early Holocene. However, a more egregious case is the direct role of atmospheric CO₂ concentration on the ratio of stomatal water loss to carbon uptake for photosynthesis, which determines the water requirement for plant growth. The reduction in water use efficiency when CO₂ is lower than today means that vegetation assemblages appear to reflect drier conditions than they actually experienced (Prentice *et al.* 2017). Statistical methods to reconstruct past hydroclimates from pollen data depend on relationships between pollen abundances and climate variables that are determined under recent atmospheric conditions (Chevalier *et al.* 2020) and cannot, by their nature, take the effect of varying CO₂ into account (Idso 1989). Recent work combining eco-evolutionary optimality modelling of plant photosynthetic traits and published experimental findings on how the ratio between CO₂ levels inside the leaf and in the air outside responds to variations in atmospheric CO₂ concentrations, however, now provides a method to correct pollen-based statistical reconstructions of moisture variables such as precipitation or plant-available moisture (Prentice, Villegas-Diaz and Harrison 2022) when atmospheric CO₂ levels were different from today. An earlier version of this method (Prentice *et al.* 2017) has been applied to correct reconstructions of reconstructed moisture during the last glacial at a single site (Wei *et al.* 2021) and used in model-data assimilation reconstructions of the Last Glacial Maximum (Cleator *et al.* 2020).

Statistical techniques are also affected by the availability and appropriateness of the modern training data set. The choice of the training data set determines the range of climate sampled and thus the range of changes that could be reconstructed from the fossil record

(Turner *et al.* 2020). Most modern data sets are regional in scope and in some cases, such as the training data sets used for reconstructions based on chironomids and diatoms, limited to small sub-continental regions. While it has been argued that more local or regional training data sets yield reconstructions with lower errors (e.g. Dugerdil *et al.* 2021), differences between, for example, pollen-based and chironomid-based temperature reconstructions at individual sites have been attributed to differences in the scope of the climate sampled by the relevant training data sets (Rosén *et al.* 2003; Holmes *et al.* 2011; Liu *et al.* 2021). The development of more extensive modern training data sets, sampling a wider range of climate, would provide a more robust way of reconstructing past climate and indeed a number of efforts are underway to produce data sets extending the geographic area sampled (e.g. the Eurasian Modern Pollen Dataset, Davis *et al.* 2020).

A further issue that affects the ability to reconstruct climates radically different from today is the tendency for statistical methods, and particularly regression-based techniques, to compress reconstructions towards the centre of the sampled climate range, such that values reconstructed from the training dataset tend to be higher than observed values at the low end, and lower at the high end. A new approach that takes account of the climatic tolerance of individual taxa and the frequency of the sampled climate in the training data set (Liu *et al.* 2020), applied within the framework of Weighted Averaging Partial Least-Squares regression, has been shown to reduce this compression bias (Fig. 2) when applied to pollen data from Europe. The reduction of the compression bias has a noticeable impact on down core reconstructions of climate through time, leading to the recognition of greater climate variability than would be apparent from standard statistical approaches (Fig. 3).

Vegetation Reconstructions

Approaches to vegetation reconstruction have undergone a similar evolution from qualitative interpretations of fossil pollen or plant macrofossil records towards quantitative approaches. One of the most widely used methods of vegetation reconstruction, biomisation (Prentice *et al.* 1996), is semi-quantitative in that it calculates similarity scores between pollen assemblages and vegetation types (biomes) but relies on expert knowledge of the regional flora to group plant taxa to plant functional types (PFTs) defined in terms of life form, leaf type, phenology and climate tolerance. Biomes are then defined as assemblages of PFTs, where the PFTs represent either the dominant or most characteristic taxa present in a specific biome. Although biomisation produces robust regional vegetation reconstructions (e.g. Prentice *et al.* 2000 and references cited therein; Bigelow *et al.* 2003; Pickett *et al.* 2004; Marchant *et al.* 2009), the subjective choices made in allocating taxa to PFTs and PFTs to biomes necessitate an iterative approach to classification. Furthermore, the biomisation method uses an *ad hoc* approach to account for the non-linear relationship between pollen assemblages and vegetation cover because of the differences in pollen production between species and differences in pollen capture because of differences in site characteristics. There are methods that account for variability in pollen productivity between species and the influence of pollen transport on pollen assemblages, such as the Landscape reconstruction Algorithm (LRA) and the REVEALS pollen transport model (Sugita 2007a; 2007b), but they are extremely data demanding and have not been applied widely. A final issue with the biomisation approach is that it does not readily identify vegetation types which are not present on the landscape today, so-called non-analogue vegetation.

Various modern analogue techniques (MAT) have also been developed and applied to reconstruct past vegetation (e.g. Overpeck, Webb and Prentice 1985; Overpeck, Webb and Webb 1992; Jackson *et al.* 2000; Janska *et al.* 2017; Chytrý *et al.* 2019). These approaches use modern training datasets to establish relationships between pollen abundances and biomes, and then use these relationships to reconstruct biomes for a fossil pollen assemblage. Decisions about the number of analogues for each reconstruction are often arbitrary and, although threshold values have been used to distinguish between different biomes, the choice of threshold is scale dependent (Gavin *et al.* 2003). Furthermore, by focusing on a limited number of analogues, potential within-biome variability is ignored. Both MAT and biomisation are sensitive to small changes in pollen abundance, which can produce apparent rapid and unrealistic shifts in biome assignments downcore, the so-called “flickering switch” problem (Allen, Watts and Huntley 2000; Fyfe, Woodbridge and Roberts 2018).

Many of these issues have been addressed in a recently developed method that combines the relative simplicity of biomisation with the more rigorous basis of statistical reconstructions (Cruz-Silva *et al.* 2022). This new technique assigns modern pollen samples to a biome based on the observed within-biome means and variability (standard deviations) in the abundances of the pollen taxa. These values are then used to calculate a dissimilarity index between any fossil pollen sample and every biome, and thus assign the sample to the most likely biome. The modern data set is also used to determine threshold values to determine when fossil pollen samples are unlike any modern biome, and this can be used to identify non-analogue vegetation types in the fossil record. Application of this new method to sites from the Eastern Mediterranean-Black Sea Caspian Corridor (EMBSecBIO) region, for example, shows that many records were characterised by non-analogue vegetation during the transition into the Holocene (Fig. 4). However, modern vegetation types are recognised in the Holocene and the records show coherent changes from open vegetation towards closed forests initially and giving way more open landscapes in the last few thousand years (Fig. 4).

Fire reconstructions

There are multiple sources of data that provide information about wildfires in the past. Ice-core records of substances emitted during biomass burning, including methane, carbon monoxide, levoglucosan, black carbon and vanillic acid (for review see Rubino *et al.* 2016) provide a record of changing fire that is either globally integrated, in the case of the well-mixed atmospheric gases, or are geographically integrated at the continental or hemispheric scale. At the other extreme, fire scars, registered as disruptions to the annual increments of tree growth rings in living or fossil trees, provide a highly localised indication of fire occurrence (Higuera, Whitlock and Gage 2011; Marlon *et al.* 2013). Reconstructions of fire history from fire scars have two disadvantages, however. Firstly, they only record relatively low intensity fires because high intensity fires remove the evidence by killing and destroying the trees. Secondly, these records only extend back a few thousand years. Charcoal, preserved in anoxic sediments, has the advantage that it provides a record of fires occurring within the catchment of a site and thus providing a local- to regional-scale picture of changes in fire regimes that can extend back for much longer periods, encompassing interglacial-glacial-interglacial transitions of the last climatic cycle (e.g. Marlon *et al.* 2008; Power *et al.* 2008; Danialu, Harrison and Bartlein 2010; Marlon *et al.* 2013). The latest global compilation of charcoal data, the Reading Palaeofire Database (RPD: Harrison *et al.* 2022) contains 1676 individ-

ual records from 1480 sites, with standardised Bayesian age models using the appropriate INTCAL20 calibration curve, metadata that allows pre-selection of sites of different types or basin size and discrimination between macrocharcoal and microcharcoal, thus making it possible to select the data appropriate for a given analysis.

The interpretation of sedimentary charcoal records in terms of fire histories is complicated by two issues. Firstly, charcoal values can vary by orders of magnitude between and within sites because of the broad range of record types, site characteristics and analytical techniques. Secondly, it is unclear what aspects of the fire regime influence charcoal accumulation at individual sites and thus whether the charcoal record reflects fire occurrence, area burnt, fire intensity or the completeness of combustion. The variation in charcoal values is generally dealt with through standardisation techniques, including minimax transformation, homogenisation of variance and rescaling through the calculation of z-scores (Power *et al.* 2008; 2010). Compositing of individual records to construct curves representative of regional fire histories has also proved a powerful way of minimising the idiosyncratic responses of individual records, although temporal binning of the records is necessary to reduce the impact of differences in sampling resolution on the composite curve (Marlon *et al.* 2008). Although composite charcoal curves provide a useful way of examining changes in fire through time, they are nevertheless only indications of relative changes. Attempts have been made to derive local calibrations that relate changes in charcoal quantitatively to proximity, burnt area and intensity (e.g. Peters and Higuera 2007; Leys *et al.* 2015; Hennebelle *et al.* 2020; Shen *et al.* 2022). However, it is unclear whether the amount of charcoal is determined by burnt area, which is a measure of fire size and fire return time, or whether it is influenced by the amount and type of biomass combusted which is largely determined by fire intensity. Recent work suggests that measurements of charcoal size and shape (e.g. Crawford and Belcher 2014; Pereboom *et al.* 2020; Feurdean 2021) or reflectance (e.g. Hudspith *et al.* 2015; Belcher *et al.* 2018) provide independent information about the material burnt and fire intensity and could be combined with charcoal values to derive a more complete understanding of past fire regimes.

Land use reconstructions

Human impact on the environment is reflected in changes in land use. Changes in land use have been inferred from pollen data, either directly in terms of the occurrence of crop pollen or other non-native adventive species (e.g. Behre 1981; 1988) or by increased frequency of native pollen types indicative of disturbance such as *Plantago* (e.g. Behre 1981; Lang 1994; Tinner *et al.* 2003). Unfortunately, many crops produce limited pollen; crops other than cereals are found only rarely in most pollen records and thus our picture of change in land use based on pollen may be incomplete (Trondman *et al.* 2015). Increases in pollen characteristic of disturbance can also reflect natural disturbance, through fires or windthrow, or indeed from climate trends towards increased aridity and more open vegetation. Various methods have been developed to reduce this uncertainty, for example by combining pollen records with archaeological evidence (e.g. Berger *et al.* 2019) or using techniques to account for the low representation of most crops using regionally specific estimates of pollen productivity (e.g. Trondman *et al.* 2015; Pirzamanbein *et al.* 2018; Cao *et al.* 2019; Githumbi *et al.* 2022). The LandCover6k project, for example, is currently using this approach to provide regional reconstructions of changes in land cover and land use during the Holocene using the REVEALS model of pollen dispersal and deposition (Sugita *et al.* 2007a, b). However,

the need for large amounts of data on pollen productivity means that these reconstructions are currently only available for Europe and some other limited regions of the world (e.g. Trondman *et al.* 2015; Pirzamanbein *et al.* 2018; Cao *et al.* 2019; Githumbi *et al.* 2022). Furthermore, there has been no consideration of the fact that the pollen productivity of early domesticates probably differed from that of modern crop varieties. Global reconstructions of land use changes, such as HistorY Database of the global Environment (HYDE: Klein Goldewijk *et al.* 2011; Klein Goldewijk *et al.* 2017) or KK10 (Kaplan and Krumhardt 2011; Kaplan *et al.* 2011) are modelled based on highly uncertain estimates of changes in population density and assumptions about land-use per capita. Differences in the underlying assumptions and uncertainties in the population estimates result in very large differences between the different land use reconstructions, and thus large uncertainties in the timing and magnitude of land use changes both regionally and at a global scale (Gaillard *et al.* 2010; Kaplan *et al.* 2017; Harrison *et al.* 2020). Again, the LandCover6k project is seeking to address this by incorporating archaeological data, such as the date agriculture is first adopted in a region and ethnographic information about land-use per capita, in the framework of these global models (Harrison *et al.* 2020; Morrison *et al.* 2021).

Population reconstructions

Global land-use reconstructions, such as HYDE and KK10, use historical estimates of absolute population levels but population estimates before the 1700s are extremely uncertain (Klein Goldewijk *et al.* 2011). Indeed, for many regions of the world, population estimate for earlier times in the Holocene are either lacking or vary wildly from one another (e.g. Harrison *et al.* 2020). Several alternative approaches to estimate population have been developed based on using archaeological data, including skeletal age data (McFadden 2021) and settlement or house size data, where the number of people per area is derived from ethnographic information (see reviews in Kaplan, Krumhardt and Zimmerman 2009; Ruddiman and Ellis 2009). The most widely used technique is to reconstruct relative changes in population size based on the quantity of radiocarbon-dated archaeological material (Rick 1987; Robinson *et al.* 2019). This approach is based on the idea that the number of dated samples reflects the amount of material produced at any time and this in turn is dependent on the number of people. The dated samples are then used to estimate relative changes in population size through creation of a summed probability distribution (SPD) of aggregated calibrated dates through time. There are known limitations of the SPD approach to estimating population including biases in sampling of archaeological sites (e.g. Torfing 2015) and in the sampling intensity of radiocarbon dates through time (Crema and Bevan 2021). Calibration of the radiocarbon dates can also induce artificial peaks or smoothing of the SPD curve (Crema and Bevan 2021). These limitations can be overcome to some extent by testing whether the resulting SPD deviates significantly from a null model of growth (Shennan *et al.* 2013; Timpson *et al.* 2014). Combining the SPD approach with other sources of information or using models of population dynamics (e.g. Porčić and Nikolić 2016) and/or resource base constraints (e.g. Freeman *et al.* 2020) in a Bayesian framework also appears to offer the possibility to reconstruct plausible and robust estimates of changing population.

Modelling tools

Models are tools that encapsulate our current understanding of different components of the natural world. Climate models, for example, draw on our understanding of fluid dynamics to simulate atmospheric and oceanic circulations and from this predict changes in local weather patterns and climate in response to changes in forcing. Although models vary in complexity and the range of processes that they seek to simulate, there are a number of common features, notably the need to simplify the system they represent because of lack of knowledge, issues of spatial or temporal resolution, or computational costs. Models can therefore be thought of as hypothesis-testing tools (Harrison, Bartlein and Prentice 2016). One of the earliest uses of climate models, for example, was to examine whether changes in insolation consequent on changes in the Earth's orbit through time were sufficient to explain the observed waxing and waning of the northern African monsoon (Kutzbach and Street-Perrott 1985). When there are multiple factors that can influence a given phenomenon, models can be used to assess the impact and relative importance of individual factors and how these might vary spatially or through time. Fig. 1, for example, shows how a simple statistical model can be used to test the importance of human activities on fire regimes and the degree to which this varies in different types of vegetation.

Statistical models

Multivariate statistical techniques are widely used to explore the relationships between environmental factors and responses to these factors and these analyses form the basis for developing simple statistical models. Generalised linear modelling, for example, has been used to investigate the controls on daily weather patterns (e.g. George, Letha and Jairaj 2016; Chandler 2020), vegetation distribution (e.g. Guisan, Weiss and Weiss 1999; Schwarz and Zimmermann 2005) and wildfires (e.g. Bistinas *et al.* 2014; Haas, Prentice and Harrison 2022) under modern day conditions. Although similar investigations can be done using machine learning techniques (e.g. Hengl *et al.* 2018; Kuhn-Régner *et al.* 2021), one advantage of generalised linear models (GLMs) is that they allow the underlying relationships with individual predictor variables to be diagnosed, even when there are correlations or interactions between variables, and displayed via partial residual plots. The form of these plots shows the nature of the relationship after the effects of other predictors are taken into account. The strength of these (positive or negative) relationships, as measured by the t-value, determines the relative importance of the predictor in the model. For example, analyses of GLMs created separately for burnt area, fire size and fire intensity (Fig. 5) but using the same set of predictor variables (climate, vegetation, ignition sources and human impacts on landscape fragmentation) show that climate and vegetation variables are more important controls on burnt area than ignitions or measures of landscape fragmentation. This plot also shows that the impact of a specific variables on burnt area may be different from the impact of that variable on fire size or intensity. Vegetation productivity, as measured by gross primary production (GPP), has a positive effect on burnt area but a negative effect on fire intensity and does not have a significant effect on fire size (Fig. 5). Once developed for modern conditions, GLMs can be used to simulate future or past states. However, the power of these relatively simple types of model to predict the past has yet to be exploited.

Vegetation and crop models

Simple biogeography, or biome, models (Prentice *et al.* 1992; Haxeltine and Prentice 1996; Kaplan *et al.* 2003) were developed to predict vegetation distribution at a global scale based on defining the climatic limits of a small number of PFTs using known physiological constraints on their growth and then applying a dominance hierarchy to determine how these PFTs are aggregated into biomes. Biome models are therefore essentially static in nature and do not model competition between PFTs explicitly. Dynamic global vegetation models (DGVMs) explicitly account for disturbance and competition (e.g. Sitch *et al.* 2003; Krinner *et al.* 2005; Kelley, Harrison and Prentice 2014). However, they preserve many of the underlying assumptions of biome models in that the properties of the vegetation at a given location are determined by competition between the plants that could grow there as determined by basic physiological constraints. Furthermore, most DGVMs use a limited number of PFTs, generally delineated in terms of life form (e.g. tree or grass), leaf form (e.g. broadleaf or needleleaf), phenology (e.g. evergreen or deciduous) and climatic limits (e.g. tropical, temperate, boreal), although there are some models (e.g. LPJ-GUESS: Smith, Prentice and Sykes 2008) that use a limited number of species representative of these PFTs for regional applications. Both biome models and DGVMs have been used to simulate the vegetation response to climate changes in the past (Prentice *et al.* 1993; Harrison *et al.* 1998; Kaplan *et al.* 2003; Ni *et al.* 2006; Ciais *et al.* 2011; Prentice, Harrison and Bartlein 2011), and to discriminate between the impact of climate and the direct physiological control of changing atmospheric CO₂ on vegetation productivity (e.g. Harrison and Prentice 2003; Martin Calvo and Prentice 2015). Originally, DGVMs represented disturbance generically but many models now include an explicit representation of fire disturbance (Rabin *et al.* 2017), allowing exploration of climate and climate-induced vegetation changes on fire regimes, as well as climate-induced changes in disturbance on vegetation, in the past (e.g. Martin Calvo, Harrison and Prentice 2014; Martin Calvo and Prentice 2015). Several DGVMs now simulate the growth of specific crops (e.g. Bondeau *et al.* 2007; Levis *et al.* 2012), although the distribution and growing season for each crop type is pre-determined and thus there is no competition and growth is solely determined by climatic and soil conditions.

DGVMs have many uses and are a necessary component of Earth System Models. Nevertheless, several problems have become apparent in recent years. DGVM predictions of future changes in vegetation cover and carbon fluxes diverge considerably and indeed this is considered one of the most important sources of uncertainty in projections of future climate (Ciais *et al.* 2013; Arora *et al.* 2020). Modellers have sought to reduce this divergence by introducing new processes, for example an explicit treatment of the nitrogen cycle (e.g. von Bloh *et al.* 2018), but with little success. Indeed, the increasing complexity of DGVMs and land-surface models itself leads to additional problems since the models require specification of an ever-increasing number of parameters most of which are currently poorly known from observations (Prentice *et al.* 2015; Franklin *et al.* 2020). Increases in model realism through representing additional processes has often led to a reduction in predictive power because of the increase in uncertainty. In addition, the fact that most DGVMs continue to represent vegetation as a collection of a limited number of PFTs is problematic since it hides the considerable variation in key functional traits within each PFT (Kattge *et al.* 2020) and the potential for the observed variation in these traits along environmental gradients to be influenced by short-term acclimation and longer-term adaptation to environmental conditions (Siefert *et al.*

2015). Many groups are now exploring new approaches to modelling vegetation, including trait-based modelling (e.g. Scheiter, Langan and Higgins 2013) and the use of eco-evolutionary optimality (EEO) theory to develop new and simpler process representations (e.g. De Kauwe *et al.* 2015; Ali *et al.* 2016; Mengoli *et al.* 2022). EEO approaches to fundamental processes, such as photosynthesis, primary production, dark respiration, stomatal behaviour and the carbon economics of leaf type, have been developed and shown to perform better than existing models (Harrison *et al.* 2021). This opens up the possibility of using these much simpler models to explore the factors influencing vegetation patterns in the past.

EEO approaches are particularly powerful in terms of crop modelling since they can be used to predict not only growth and yield (Qiao *et al.* 2020; 2021; Yuwono 2021) but also the optimal timing of the growing season to maximise yields (Qiao *et al.* 2022). This is particularly important because the models currently used to predict crop yields under climate change, for example as part of the Inter-Sectoral Impact Model Intercomparison Project, ISIMIP2b: <https://www.isimip.org/protocol/#isimip2b/>) necessarily specify the planting and harvest dates based on current conditions, even though there is already evidence that farmers are adjusting to current climate changes (e.g. Olesen *et al.* 2012; Hunt *et al.* 2019). The comparison of EEO-based model predictions of potential yield compare well with observations of potential wheat yield in 2000 CE from EARTHSTAT (www.earthstat.org), both in terms of spatial patterns and in overall magnitude (Fig. 6). In fact, Qiao *et al.* (2021) show that this simple EEO-based model performs better than the more complex models in ISIMIP - most of which underestimate potential yield either over substantial regions of the world or globally. Sensitivity experiments examining the impact of climate change from changes in climate and atmospheric CO₂ concentration combined (Fig. 6) show that the positive effects of CO₂ fertilisation on plant growth offset the negative impacts of higher temperatures over much of the world. The importance of CO₂ fertilisation on crop growth under current conditions raises the question of whether the increase in CO₂ during the deglaciation into the Holocene was instrumental in facilitating the adoption of agriculture (Sage 1995; Cunniff *et al.* 2010).

Climate models

General circulation models (GCMs) provide a tool to examine how regional climates have changed in response to changes in external forcing, such as the change in insolation caused by changes in the Earth's orbit. These models are based on known physics but, since they are generally run at relatively coarse spatial resolution (*ca* 2 x 2°) to reduce computational costs, processes that operate at finer resolutions are represented in a simplified way through parameterisations. One example of this is that most GCMs do not resolve individual clouds or within-cloud processes like droplet formation explicitly, but instead describe the aggregate behaviour of clouds within a grid cell. The earliest GCMs only described the behaviour of the atmosphere (e.g. Gates 1976; Manabe and Hahn 1977; Kutzbach and Guetter 1986) and other elements of the climate system, such as sea-surface temperatures and vegetation, were prescribed from observations. However, there has been a gradual evolution towards explicitly modelling all the components of the climate system such that state-of-the-art models used, for example, for future climate projections now explicitly include the circulation of the ocean, sea ice formation and dynamic vegetation. As such, they are often referred to as Earth System Models. Although the models have increased in complexity, there are still climate processes that are not included in most models, such as ice sheet dynamics or ocean biology.

Furthermore, although model resolution has increased, parameterisation is still required for sub-grid scale processes in the ocean and on land.

The computational costs of running complex Earth System Models has meant that, until recently, most palaeoclimate simulations were snapshots of specific time periods such as the Last Glacial Maximum (conventionally defined as 21,000 years ago) or the mid-Holocene (6000 years ago). The Palaeoclimate Modelling Intercomparison Project (PMIP: Kageyama *et al.* 2018) has coordinated international efforts to produce snapshot simulations of key times in the past to understand the mechanisms of past climate changes, to compare different models to gain insights into the uncertainties of their predictions, and to evaluate model performance (Braconnot *et al.* 2012; Harrison *et al.* 2014; Schmidt *et al.* 2014; Harrison *et al.* 2015). PMIP has evaluated model performance through multiple phases of model development, from simple atmosphere-only models through to the current generation of Earth System Models, and these evaluations indicate the extent to which models that are used for future climate projections capture large climate changes (e.g. Brierley *et al.* 2020; Kageyama *et al.* 2021). Snapshot simulations have also been used to test hypotheses about the triggers for observed climate changes, for example the role of changes in orbital forcing and land-surface feedbacks in modulating the monsoons (Kutzbach *et al.* 1996; Claussen and Gayler 1997; Braconnot *et al.* 1999; Levis, Bonan and Bonfils 2004; Vamborg, Brovkin and Claussen 2011; Krinner *et al.* 2012; Swann *et al.* 2014), the role of meltwater discharge into the North Atlantic on causing abrupt events during the last glacial or the recent deglaciation (Morrill *et al.* 2014; Kageyama *et al.* 2013; Menviel *et al.* 2014), and the impact of anthropogenic changes in land-surface conditions on climate during the Holocene (He *et al.* 2014; Smith *et al.* 2016). These simulations are not necessarily realistic: the magnitude of the freshwater inputs required to generate a shut-down of the Atlantic meridional overturning circulation in a model, for example, is usually much larger than the actual inputs associated with abrupt climate events. Nevertheless, they are useful ways to explore specific hypotheses about the mechanisms involved.

Time-varying or transient simulations are increasingly being used to explore past climates. Transient simulations of the millennium prior to the industrial revolution provide a way of examining decadal to centennial climate variability in a climate state relatively similar to the present and determining the relative importance of internal stochastic processes and external forcings in generating this variability (Jungclauss *et al.* 2017). These simulations are therefore important for detection-attribution studies and provide the context for current and future climate changes (Masson-Delmotte *et al.* 2013). Although climate changes in the last millennium have been relatively small compared to earlier palaeoclimate intervals, they have nevertheless left their imprint on human history (Büntgen *et al.* 2016; Xoplaki *et al.* 2016; Camenisch *et al.* 2016), and thus the transient simulations of the last millennium can help to identify plausible mechanisms underpinning these impacts through sensitivity experiments examining the role of individual forcings (Jungclauss *et al.* 2017).

Transient climate simulations have now been run for periods before the last millennium, including relatively coarse-resolution simulations from the Last Glacial Maximum to the present-day (Liu *et al.* 2009), and higher-resolution simulations of the last deglaciation (e.g. Kapsch *et al.* 2022; Snoll *et al.* 2022) and the latter part of the Holocene (Braconnot *et al.* 2019; Crétat *et al.* 2020; Dallmayer *et al.* 2020). These simulations allow us to explore the relationship between long-term multi-millennial trends and decadal to centennial variability.

ty (Carré *et al.* 2021) and how this variability influences the prevalence of climate modes (Créat *et al.* 2020). They have also been used to explore both forced abrupt events (e.g. 8.2ka: Tindall and Valdes 2011; Matero *et al.* 2017) and the potential for abrupt events to be generated by internal unforced variability (Drijfhout *et al.* 2013; Gottwald 2020). However, the existence of unforced variability is a challenge in terms of comparisons of simulated and observed climate changes since there is no expectation that these will be registered at the same time: observations document the actual, realised climate changes while models represent one of the many climate trajectories that could have occurred. Thus, these simulations need to be analysed in terms of the strength and frequency of variability and how these change under different forcings or are affected by different feedbacks. Nevertheless, transient simulations provide an invaluable tool for interpreting palaeoenvironmental records. Such simulations, for example, show marked difference in precipitation and temperature change across Europe and the Middle East during the mid-Holocene (Fig. 7), with increased precipitation in southern Europe contrasting with drier conditions compared to present in northern Europe (Fig. 7a) and less marked warming on the maritime fringe of western Europe compared to large changes in temperature further east (Fig. 7b). The simulated longterm trends in precipitation and summer (June, July, August) temperature vary regionally (Figs. 7c, d, e); comparing these trends with $\delta^{18}\text{O}$ records from speleothems suggests that the speleothem records in the Middle East predominantly reflect changes in precipitation while those from northern Europe reflect changes in temperature. Both the speleothem records and the simulated climate exhibit multi-centennial variability, which is broadly similar across all of the regions but considerably more muted in the simulations than in the speleothem records, suggesting that in the real world this variability is enhanced by forcings or feedbacks not captured in the model simulations.

Case study: the Holocene of Iberia and potential human impacts

We use the Iberian Peninsula as a case study to show how these various tools can be used to address questions about climate-human interactions since there are now independent reconstructions of climate, population and fire regimes for this region through the Holocene. Pollen-based climate reconstructions using an updated version of fxTWA-PLS (fxTWA-PLSv2: Liu *et al.* 2021) show a gradual increase in winter temperature over the Holocene (Fig. 8a), consistent with changes in winter insolation forcing. This trend is also seen in transient climate model simulations over the latter part of the Holocene (Fig. 8d). Climate changes in summer are not related in a straight-forward way to the changes in summer insolation. Rather there is a marked peak in plant-available moisture between *ca* 10,000 and 6000 yr B.P. (Fig. 8c) and this interval is characterised by somewhat warmer but relatively stable summer temperatures (Fig. 8b). Liu *et al.* (2021) attribute the wetter conditions in the early- to mid-Holocene to increased moisture advection into the interior of Iberia, which implies changes in atmospheric circulation, and argue that feedbacks associated with the increased moisture would have moderated the direct response to changes in summer insolation. The Iberian Peninsula is characterised by a steep west-east moisture gradient today, and the absence of such a strong gradient in the early- to mid-Holocene has implications for the development of natural vegetation and fire disturbance. Indeed, reconstructions of burnt area (Fig. 8e; Shen *et al.* 2022) show that the mid-Holocene was characterised by low fire activity and peaks in burnt area around *ca* 11,500 yr B.P. and in recent millenium correspond with times that are relatively

dry. Comparison of the burnt area reconstructions with estimates of population based on summer probability distributions of radiocarbon dates on archaeological material (Fig. 8f; Sweeney, Harrison and Vander Linden 2022) suggest there is no direct correlation between times of rapid population growth, around 7400 and 5400 yr B.P., with either climate changes or fire. Sweeney, Harrison and Vander Linden (2022) argue that the lack of correlation with changes in fire regime suggests that human impacts on the landscape were of relatively minor importance compared to climate. However, there is no obvious signal of the impact of climate changes on fire regimes, although this may reflect the coarse resolution of the climate reconstructions and the fact that they are a composite signal for the whole of the Iberian Peninsula. A more nuanced examination of the impact of changes in the west-east moisture gradient on fire regimes would be useful here. The reduced west-east moisture gradient in the early- to mid-Holocene also has implications for the resources available for people, since it would render parts of the Peninsula more suitable for human habitation and agriculture. It is interesting to speculate whether the wetter conditions in central and eastern Iberian during the early- to mid-Holocene influenced the timing of the Neolithic transition across the region, given that the earliest adoption of agriculture occurred in the south and east of the Peninsula (Isern *et al.* 2014; Drake, Blanco-González and Lillios 2017).

Perspective: examining climate-human interactions and inter-community synergies

An understanding of the complex interactions between climate and humans requires a multi-disciplinary approach, involving independent reconstructions of climate, environmental changes, and the intensity of human activities at a continental scale. The existing data coverage across the Middle East and Europe for any of these is uneven, so a systematic analysis would require a considerable improvement in the spatial and temporal coverage of reconstructions of climate, vegetation, fire and human activities. One issue, particularly for reconstructions of population based on radiocarbon dates, is to ensure that the sampling approach is consistent between different regions. Exploration of alternative sources of information for each of these parameters would be useful. In the case of the reconstruction of fire, for example, it would be useful to explore the emerging techniques for reconstructing fire intensity as a way of improving the interpretation of changes in charcoal abundance. The combination of pollen data and archaeological information to reconstruct the growth of agriculture and the intensity of human impacts on natural vegetation also appears to be a promising avenue to pursue. Any comparison of multiple reconstructions must be based on rigorous statistical approaches to data analysis. One issue in combining different data sources on climate, environmental changes and human activities is to include the propagation of uncertainty. While uncertainties in age models are routinely considered, there is less consideration of the statistical uncertainties associated with the individual reconstructions.

Models can be used to investigate how things might change, for example, how climate might change in response to changes in insolation forcing or how crop yields might change in response to warming. However, the outcomes of such model experiments are crucially dependent on the accuracy of the inputs and the quality of the model. Changes in insolation are well known, for example, but changes in land cover and land use are not well known globally. Thus, simulations to test the impact of land cover and land use on climate will produce predictions that differ considerably because of the uncertainties in the input data sets. Furthermore, the models themselves produce different results and do not necessarily capture observed

changes accurately. However, there is a role for climate, vegetation and crop models as tools for hypothesis testing. Crop models can be used, for example, to test whether the growth of a particular crop was constrained by climate conditions at a particular time or was limited by the availability of nutrient inputs. Fire-enabled vegetation models could be used in a similar way to test whether changes in fire regimes were a response to changes in moisture availability or changes in temperature by perturbing individual inputs. In hypothesis-testing mode, model inputs do not have to be realistic — for example, climate inputs could be perturbed proportionally and the realism of the results assessed by comparison with observations. In a similar way, the impact of nutrient supply on crop growth could be investigated by using plausible scenarios of management practices. However, in using models as hypothesis-testing tools, it is important to consider the generalisability of the results and the possibility that they are influenced by differences in the scale of the models and the observations used as a constraint.

No matter whether we approach the interactions between humans and their environment through a rigorous statistical analysis of multiple types of observations or through using model experiments to test specific hypotheses, there is a need for close collaboration between diverse scientific communities — archaeologists, palaeoclimatologists and people working on other palaeoenvironmental reconstructions, and modellers. An urgent necessity is to work together to define clear questions that could be addressed given the wealth of tools that we now have available.

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Extended captions of figures

Figure 1

Impact of human activity on different properties of the fire regime in different biomes under modern conditions based on generalised linear models predicting burnt area, fire size and fire intensity as a function of climate, vegetation and measures of human activity. The biome data were derived from the Hengl et al (2018) potential natural vegetation map. The biomes are xeric shrubland (XSHB), warm temperate evergreen and mixed forest/warm-temperate evergreen needleleaf and sclerophyll broadleaf forest (WTFS), tundra (TUND), tropical savanna (TRSA), cool-temperate tropical rainforest (TRF), evergreen broadleaf forest (TREB), temperate deciduous broadleaf forest/temperate malacophyll broadleaf forest (TEDE), tropical deciduous broadleaf forest and woodland (TDFW), steppe/graminoids with forbs (GRAM), temperate woodland/evergreen needleleaf woodland (ENDW), desert (DESE), cool mixed evergreen needleleaf and deciduous broadleaf forest (CMIX) and cold deciduous forest (CENF). In pink, predictions of fractional burnt area, fire size (km^2) and fire intensity (W.m^{-1}) accounting for human influence on the landscape (population density, cropland and road density) and in blue predictions where these human influences were excluded and only climate and vegetation factors were considered.

Figure 2

Comparison of reconstructions of mean temperature of the coldest month (MTCO), growing degree days above a baseline of 0°C (GDD0) and a moisture index (α), an estimate of the ratio of actual evapotranspiration to equilibrium evapotranspiration, based on a modern training pollen data set for Europe. The left panels (a, c, e) show reconstructions of these three variables using Weighted Averaging Partial Least-Squares (WA-PLS) regression and the right panels (b, d, f) show reconstructions based on the new approach which takes account of the climatic tolerance of individual taxa and the frequency of the sampled climate in the training data set (fxTWA-PLS2). The 1:1 line is shown in black; the fitted linear regression line between observed and reconstructed values is shown in red, to show the degree of overall compression. The horizontal dashed lines indicate the natural limit of α (0~1.26).

Figure 3

Comparison of downcore reconstructions of (a) mean temperature of the coldest month: MTCO, (b) growing degree days above a baseline of 0°C : GDD0 and (c) a moisture index estimated as the ratio of actual evapotranspiration to equilibrium evapotranspiration: α , based on the Holocene pollen record from Basa de la Mora. The black lines show reconstructions made using Weighted Averaging Partial Least-Squares (WA-PLS) regression and the red lines show reconstructions using the new approach which takes account of the climatic tolerance of individual taxa and the frequency of the sampled climate in the training data set (fxTWA-PLS2). The shading shows 95% confidence intervals (reconstructions plus or minus 1.96 times their bootstrap estimates of sample-specific errors) of reconstructions using WA-PLS (black shading) and fxTWA-PLS v2 (red shading). Dashed horizontal lines show the estimate of the central range of the climate in the training dataset. Lines at 0 cal yr BP show the observed modern climate values at the site. The bar graphs show the range (maximum minus minimum) of reconstructed values over the Holocene for (d) MTCO, (e) GDD0 and (f) α using the two methods, and the numerical difference is given above each bar.

Figure 4

Downcore vegetation reconstructions through time for pollen records spanning at least 8000 years from the Eastern Mediterranean-Black Sea Caspian Corridor (EMBSecBIO) region (28° - 49°N , 20° - 62°E). The plot shows entities that have a minimum length of 500 years and a minimum mean resolution of 130 years in 1000-year windows with 50% overlap; the vegetation reconstructions are made for individual

bins of 130 years where the pollen samples were objectively assigned to vegetation types based on their similarity scores (Cruz-Silva *et al.* 2022). The biomes are tundra (TUND), desert (DESE), graminoids with forbs (GRAM), evergreen needleleaf woodland (ENWD), xeric shrubland (XSHB), cold evergreen needleleaf forest (CENF), temperate malacophyll broadleaf forest (TEDE), cool mixed evergreen needleleaf and deciduous broadleaf forest (CMIX), and warm-temperate evergreen needleleaf and sclerophyll broadleaf forest (WTFS). Samples with scores below the minimum threshold for each biome are shown as non-analogue (NON-ANALOG). The records are grouped by biogeographic regions, based on the classification of Rivas-Martínez *et al.* (2004): A) Apennino-Balkan, B) Pannonio-Carpathian, C) Euxine, D) Graeco-Aegean, E) Adriatic, F) Escitian, G) Armenio-Iranian, H) Caucasian, I) Caspian.

Figure 5

T-values of individual predictors (significant at $p < 10^{-6}$) for individual generalised linear models of burnt area (BA), fire size (FS) and fire intensity (FI) (Haas, Prentice and Harrison 2022). The predictors can be classified as vegetation load and type predictors (annual gross primary production, GPP; GPP seasonality; and the percentage cover of trees, grass and shrubs), landscape fragmentation predictors (as measured by road density; area of crops; and topographic complexity as measured by the vector ruggedness index, VRI, or the topographic prediction index, TPI), climate predictors (number of dry days, DD; seasonality of dry days; vapour pressure deficit, VPD; diurnal temperature range, DTR; wind speed, wind) and ignition predictors (number of lightning strikes, light; number of human ignitions as indexed by population density, popd). Controls of burnt area, fire size and fire intensity are shown by the strength of each relationship, either as a driver (positive relationship) or as a limit (negative relationship), where the larger the absolute t-value, the stronger the relationship.

Figure 6

Crop modelling. (a) PC model predictions of potential wheat yield in 2000 CE compared to (b) the observation-based potential wheat yield in 2000 CE from EARTHSTAT (www.earthstat.org). Model simulations of (c) the change in potential yield as a consequence of changes in climate between 2000 and 2015 CE and (d) as a result of changes in climate and CO₂ over the same interval.

Figure 7

Regional changes in annual precipitation and summer (June to August) temperature for the last 6000 years, simulated by four transient climate model simulations. The models are the MPI (Max Plank Institute) Earth system Model, the AWI (Alfred Wegener Institute) Earth system model and two versions of the IPSL (Institut Pierre Simon Laplace) model. The uppermost panels show (a) anomalies in precipitation at 6000 yr BP compared to present and (b) anomalies in summer (June, July, August: JJA) temperature at 6000 yr BP compared to present. The middle panels show the evolution of precipitation and summer temperature for (c) the Middle East, (d) northern Europe and (e) southern Europe from 6000 years BP to the present day. The simulated climate evolution can be compared to observations, here regional composites of speleothem $\delta^{18}\text{O}$ evolution. The geographic distribution of the speleothem sites is shown in (a) and (b). The speleothem composites were constructed by converting $\delta^{18}\text{O}$ values to z-scores (to standardise values) using a base period of 2,000-5,000 years BP. The overall trend is obtained by fitting a 500-year half-window loess fit and 5 and 95 % confidence intervals were obtained by bootstrap resampling by site.

Figure 8

Composite reconstructions of changes in climate, fire, and people on the Iberian Peninsula during the Holocene. The pollen-based climate reconstructions of (a) mean temperature of the coldest month (MTCO), (b) mean temperature of the warmest month (MTWA), and (c) plant-available moisture represented by α , an estimate of the ratio of actual evapotranspiration to equilibrium evapotranspiration, were

derived using fx-TWAPLS (Liu *et al.* 2021). Changes in mean winter (December, January, February) temperature (d) as simulated by four climate models, (the Alfred Wegener Institute Earth System Model: AWI; two versions of the Institut Pierre Simon Laplace Earth system model: IPSL-sr, IPSL-vlr; and the Max Planck Institute Earth System model: MPI), are shown for comparison with the reconstructed MTCO. The coloured lines show the mean temperature values for each model and the shading represents the 95% confidence interval. The reconstruction of (e) burnt area is based on a calibration of the pollen-charcoal relationship against observed modern burnt area and applied downcore (Shen *et al.* 2022). The reconstruction of (f) changes in population is based on the summed probability distribution of radiocarbon dates on archaeological material (Sweeney, Harrison and Vander Linden 2022).

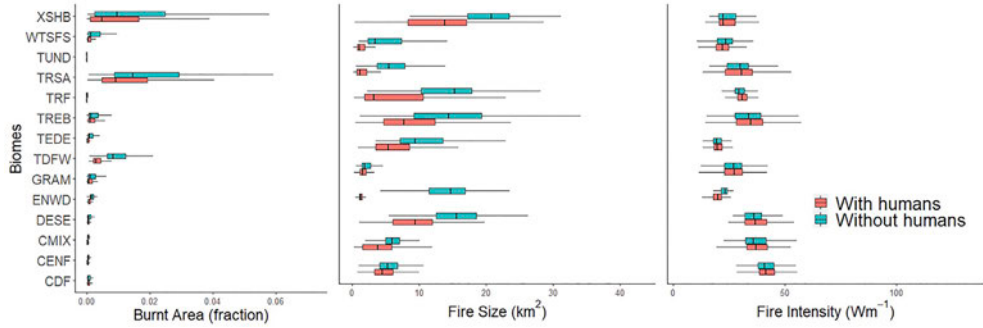


Fig. 1: Impact of human activity on different properties of the fire regime in different biomes under modern conditions. *See extended caption above*

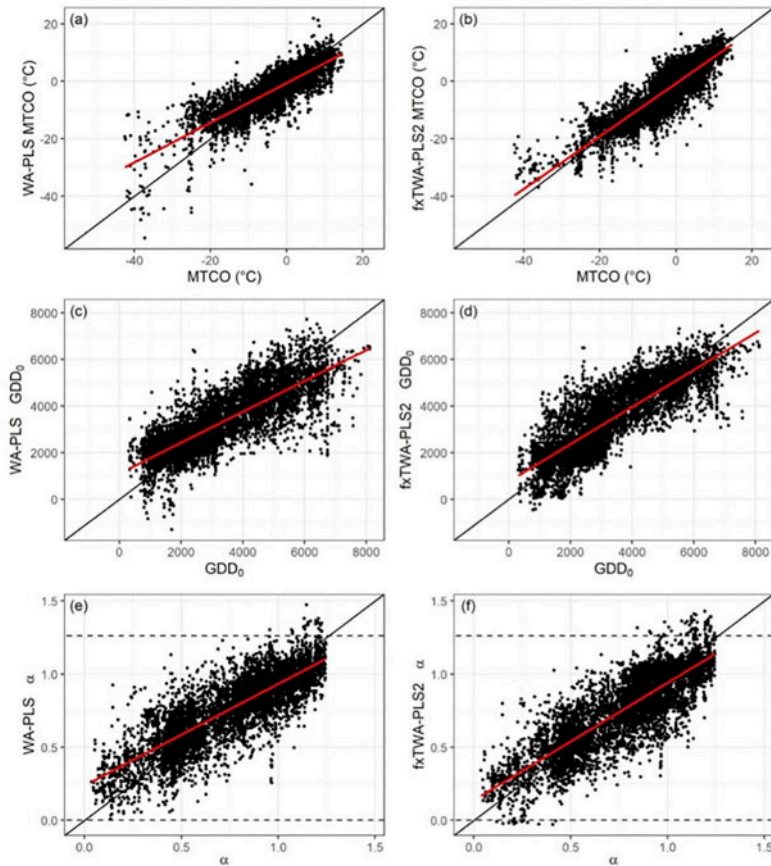


Fig. 2: Comparison of reconstructions of mean temperature of the coldest month (MTCO), growing degree days above a baseline of 0°C (GDD_0) and a moisture index (α). *See extended caption above*

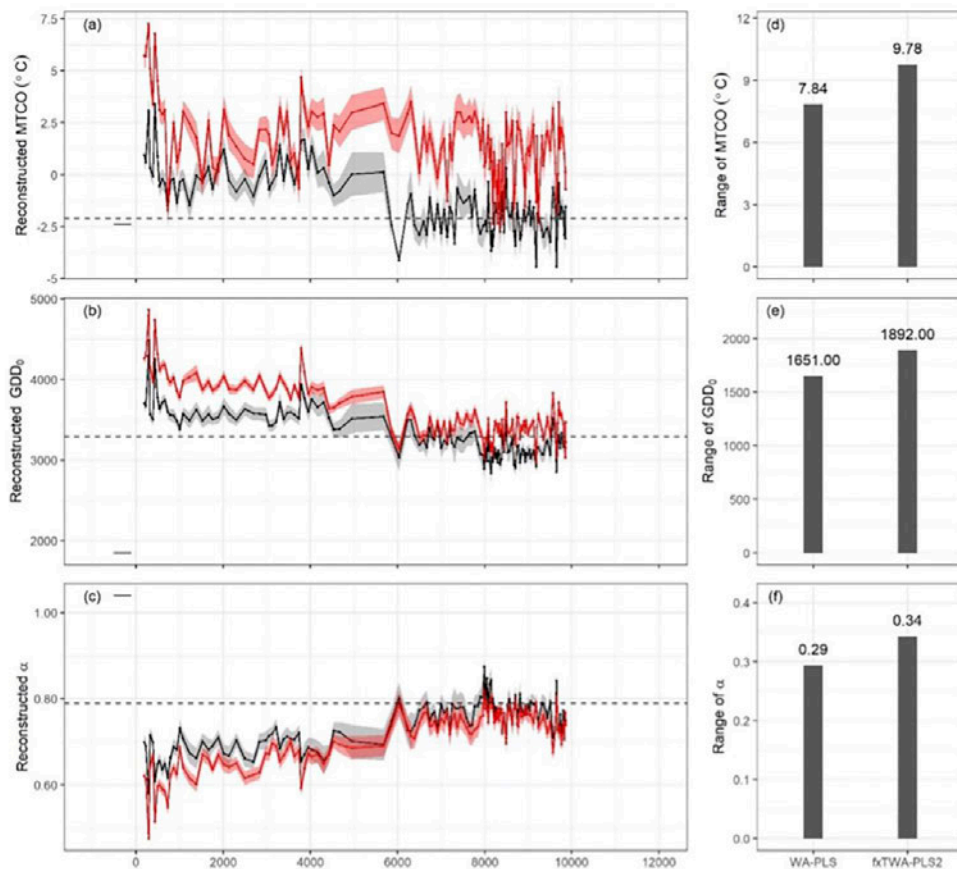


Fig. 3: Comparison of downcore reconstructions, based on the Holocene pollen record from Basa de la Mora. *See extended caption above*

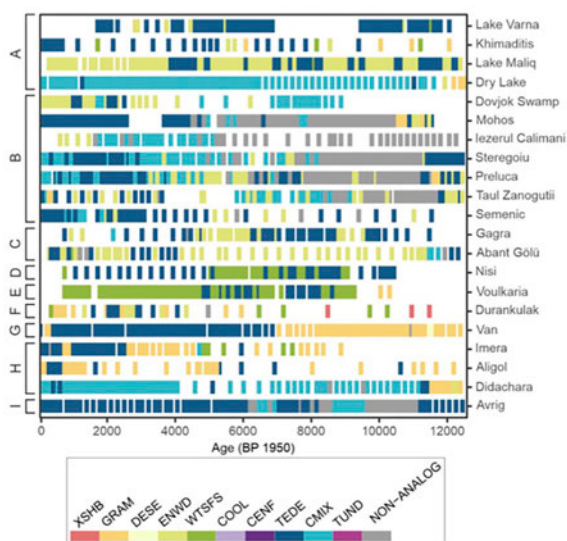


Fig. 4: Downcore vegetation reconstructions through time for pollen records spanning at least 8000 years from the Eastern Mediterranean-Black Sea Caspian Corridor. *See extended caption above*

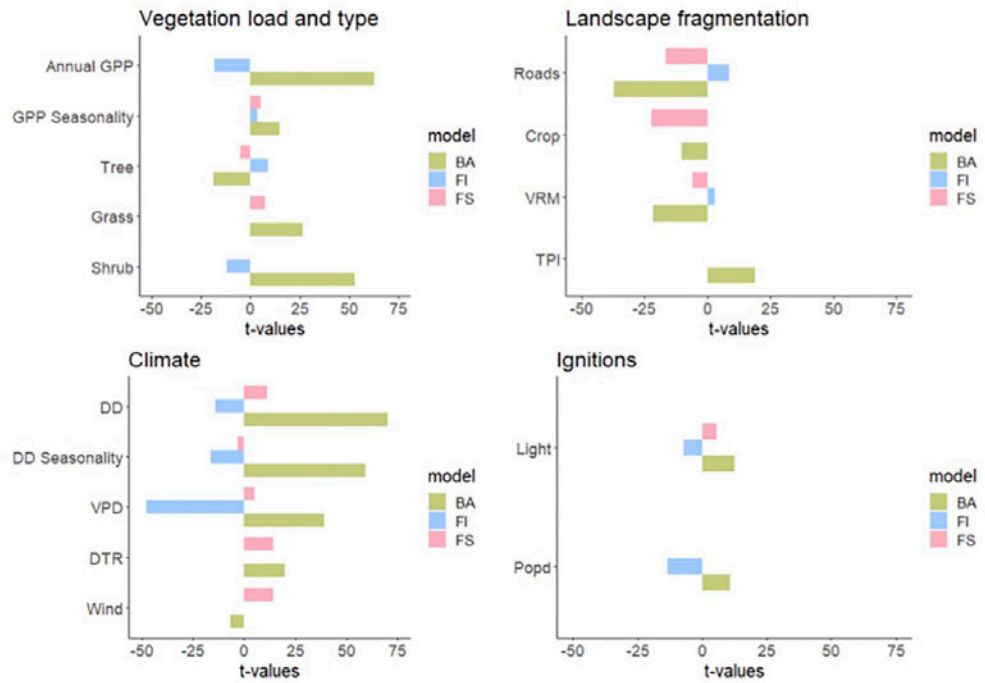


Fig. 5: T-values of individual predictors (significant at $p < 10^{-6}$) for individual generalised linear models of burnt area (BA), fire size (FS) and fire intensity (FI) (Haas, Prentice and Harrison 2022). *See extended caption above*

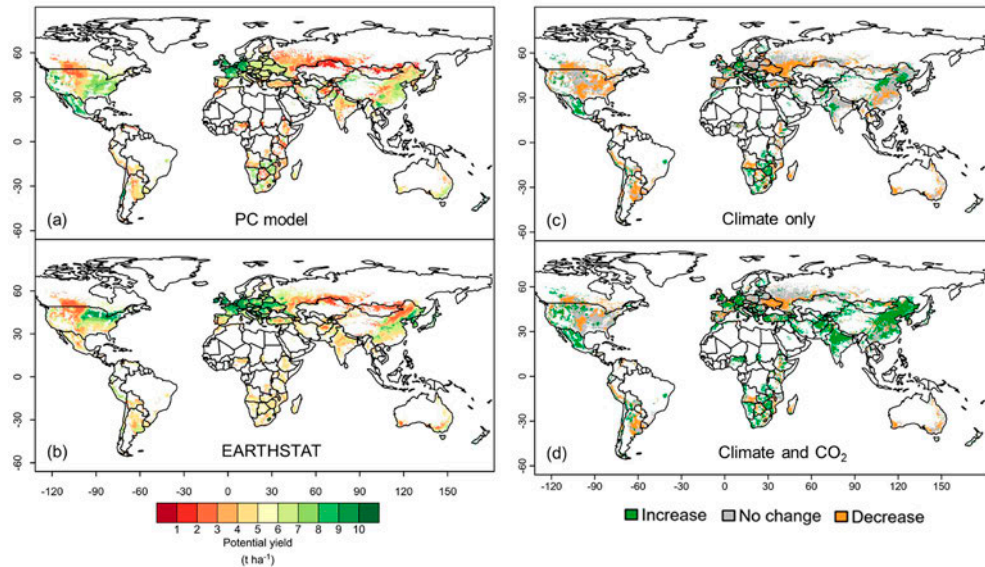


Fig. 6: Crop modelling. *See extended caption above*

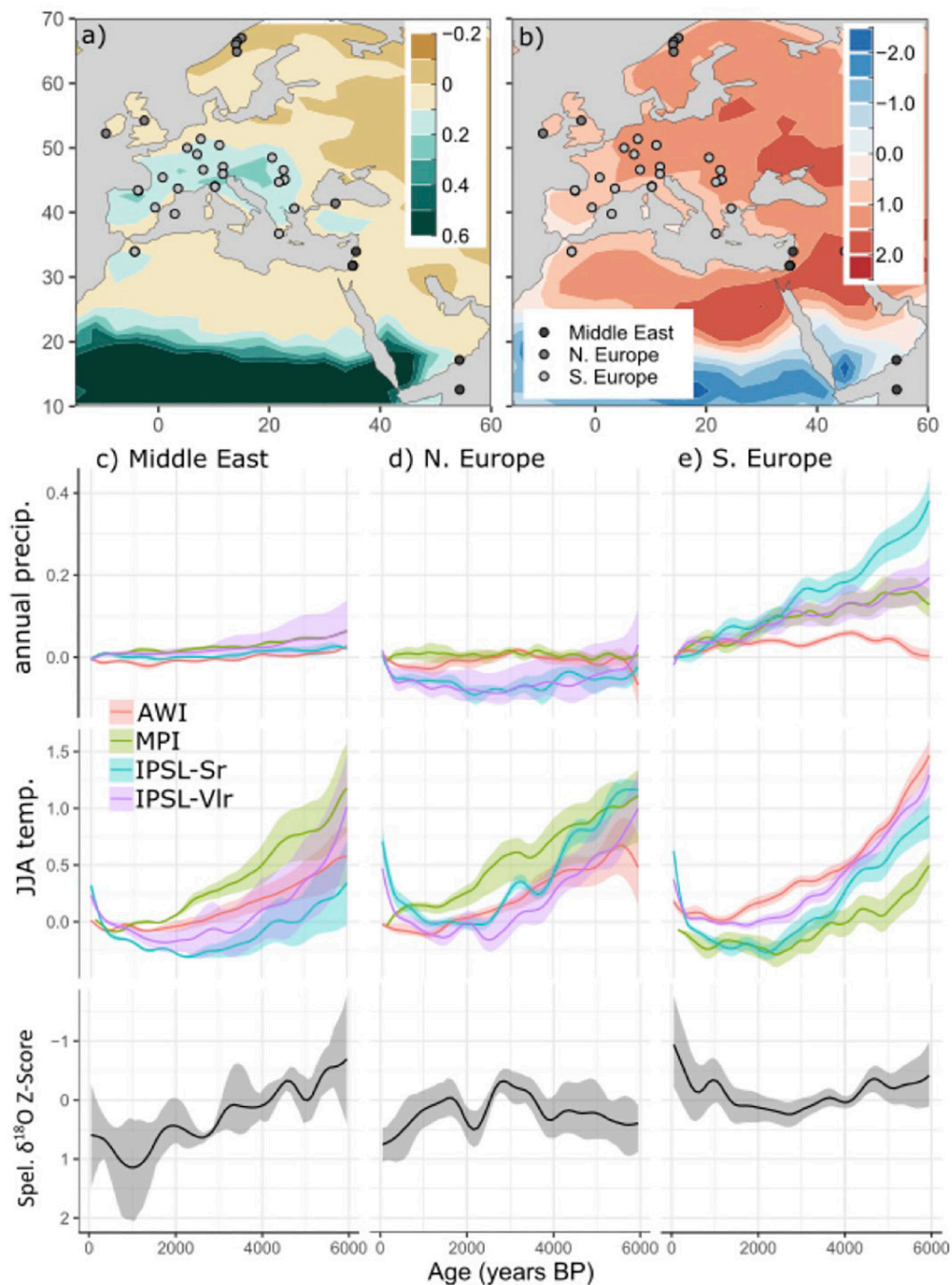


Fig. 7: Regional changes in annual precipitation and summer (June to August) temperature for the last 6000 years, simulated by four transient climate model simulations. *See extended caption above*

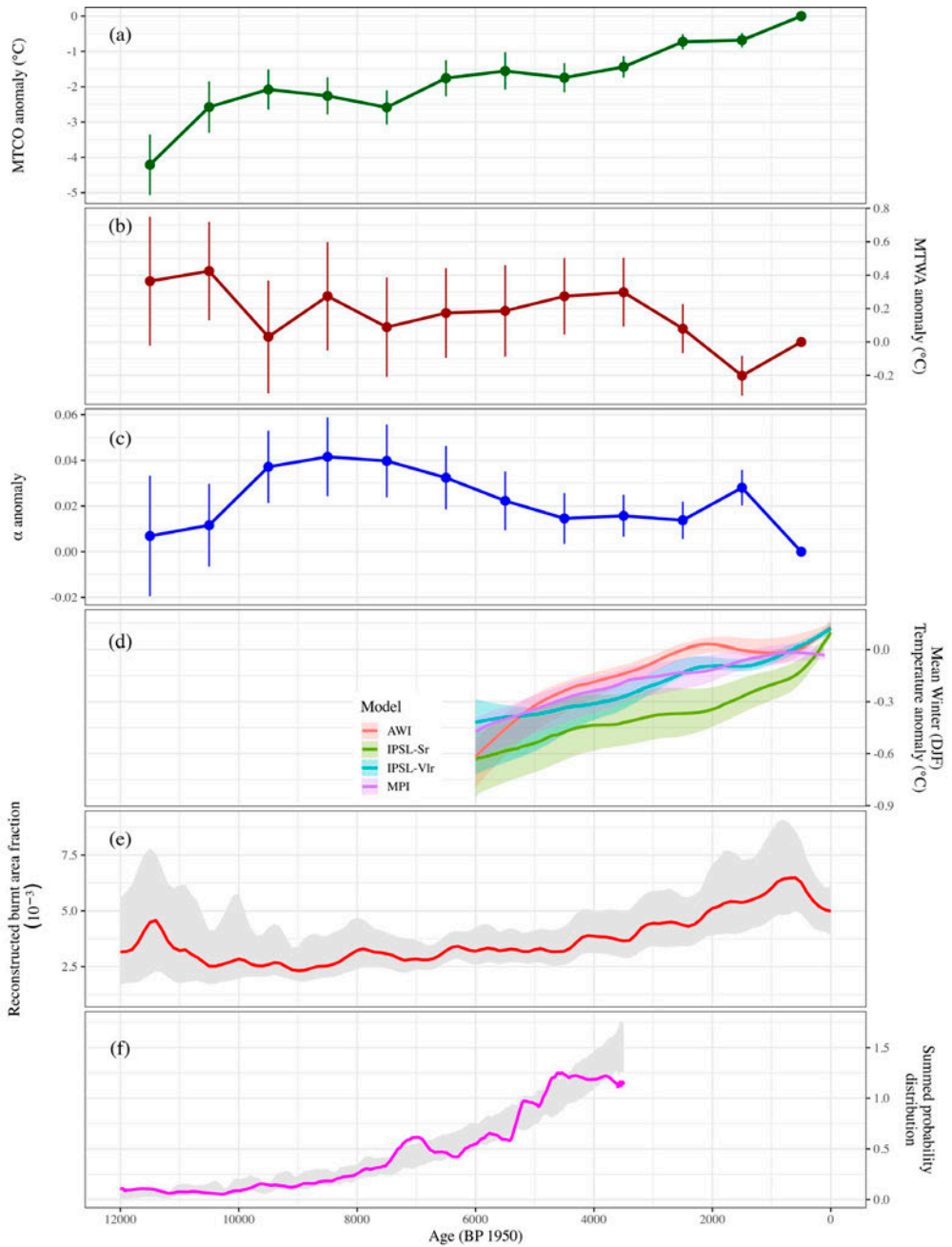


Fig. 8: Composite reconstructions of changes in climate, fire, and people on the Iberian Peninsula during the Holocene. *See extended caption above*