

# Biogeography of crop progenitors and wild plant resources over in terminal Pleistocene and Early Holocene boundary West Asia, 14.7–8.3 ka

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## Abstract

This paper presents the first continuous, spatially-explicit reconstructions of the palaeodistributions of 56 plant species found regularly in association with early agricultural archaeological sites in West Asia, including the progenitors of the first crops. We used machine learning to train an ecological niche model of each species based on its present-day distribution in relation to climate and environmental variables. Predictions of the potential ranges of these species at key stages of the Pleistocene–Holocene transition could then be derived from these models using downsampled data from palaeoclimate simulations. Species ranges are predicted to have been on significantly smaller in the Early Holocene compared to present conditions, with many species that are found throughout the region’s ‘hilly flanks’ today indicated to have much more restricted distributions centered on the Levant, Cyprus and Western Anatolia. Ranges shrunk by on average c. 10% from the terminal Pleistocene to the Early Holocene, with a further c. 10% reduction for the duration of the Younger Dryas. However, modelled ranges do not reliably predict the observed occurrence of specific species

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at archaeological sites. [...] The regional ubiquity of species in the archaeological record is [not] correlated with the predicted size of its range and the diversity of archaeobotanical assemblages is [not] correlated with the predicted diversity of its environs. This indicates that trends in taxonomic composition of the archaeobotanical record is [not] likely to have been influenced by environmental change and species turnover, in addition to human economic choices.

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- ☐ First draft:
  - ☐ Introduction
  - ☐ Background
    - ☐ Biogeography
    - ☒ ENM
  - ☒ Methods & Materials
  - ☒ Results
  - ☐ Discussion
    - ☐ General trends
    - ☐ Case studies
    - ☒ Comparison with archaeobot
  - ☐ Conclusion
- ☐ Figures
  - ☒ fig-region
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  - ☐ tbl-predictors
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- ☐ Add missing references
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- ☐ Appendix with all hindcast predictions (HTML?)
- ☐ Clean up package code
- ☐ Final proofread

## 1. Introduction

- The first farming societies had an ecological context
- Subsistence is understood (largely) through archaeobotany and zooarchaeology; ecological context from environmental archaeology, palynology, palaeoclimate records, etc.
  - But these have a variety of biases (human selection, taphonomy, etc.)
  - And at the end of the day only represent specific places – interpolation to the entire region is not straightforward
  - Overlap makes it difficult to see where human choices depart from the environmental background (cf. [Martin et al., 2016](#))
  - Or to fully contextualise subsistence strategies and shifts in strategies in response to environmental shifts (e.g. [Yaworsky et al., 2023](#)).
- Here we present an alternative approach using ENM
  - Whole region, at multiple climate snapshots
  - Independent of archaeobot. and pal. clim. data, so can verify and compare

## 2. Background

- The transition to agriculture in West Asia was...

### 2.1. *Biogeography and agricultural origins*

- Has always been important in study of agricultural origins
  - Historically: Vavilov, Pumpelly & Childe
  - Genetic studies tell us origin points, but not ranges
- Important to e.g.
  - Distinguish environmental from potentially anthropogenic change (??)
  - Reconstruct sequences of domestication (?)
- Epipal./Neo. plant-based economies were diverse
  - More than the “founder crops”;

- More than food
- (In archaeobot., not all intentionally collected)
- Geographically and temporally diverse
- ...so we model lots of species!
- Regional ecological reconstructions generally rely on the ‘expert interpolation’ (or what do they call it with isoscapes?) method
  - See CSEAS (AEA-prep) presentation
  - Figure: comparisons

## 2.2. *Ecological niche modelling in archaeology*

Ecological niche modelling (ENM) or species distribution modelling (SDM) is widely used by ecologists to predict the geographic range of a species based on a set of environmental predictors. Essentially, it involves combining records of where an organism has been observed with environmental data (climate, topography, etc.) for those locations to model the range of environmental values at which that species – its environmental niche. This model can then be used to predict the range of the organism in question either in the same or a different environment. ? suggests reserving the term ‘species distribution modelling’ for when the method is used to recover the verifiable range of a species in a real and existing environment, and using ‘ecological niche modelling’ as the broader term covering hypothetical or predictive applications – a convention we follow here when referring to predictive or ‘hindcast’ models of past ranges. Within this overarching framework, ecological niche modelling encompasses a wide range of applications and a variety of potential environmental predictors, modelling approaches, and methodologies, which we will not attempt to review here.

Ecological niche modelling has long been of interest to archaeologists as both a means of exploring the biological niche of humans and for reconstructing the past environments they inhabited (?Franklin et al., 2015). In the first sense, it has been used most extensively to model the range of humans and other hominin species (e.g. ??????), especially in the Palaeolithic. This overlaps with what archaeologists usually call generically ‘predictive modelling’ (?)—more precisely

‘site distribution modelling’—which is essentially the same approach as (and often borrows methodologies from) ecological niche modelling but applied to the occurrence of archaeological sites. Here what is modelled is not strictly a biological niche alone, but also aspects of human geography, taphonomy, and archaeological visibility. These applications can be distinguished from ‘palaeoecological niche modelling’, where the object of model remains, as in ecology, a non-human biological niche.

[Franklin et al. \(2015\)](#) review palaeoecological niche modelling and advocate for its greater adoption in environmental archaeology. In an early application to West Asia, [Conolly et al. \(2012\)](#) used the occurrence of wild and domestic *Bos* remains at prehistoric archaeological sites to map the evolving niche of cattle over the Pleistocene–Holocene transition. It has been used to model the availability of fauna exploited by humans at wider scales (e.g. ??) and, in a West Asian context, of foraged plant resources in the landscape around the Neolithic site of XX ([Collins et al., 2018](#)). Modelling the spread of crops has been another significant archaeological application (?).

In the majority of studies to date (palaeo)ecological niche modelling has been applied to archaeological data in an ‘inductive’ fashion, i.e. faunal and botanical remains from ancient sites are used as the occurrence dataset for training a model using either past or present environmental data. However, both the zooarchaeological and archaeobotanical records are sparse and subject to a complex array of depositional, taphonomic and recovery biases factors that , many of which are not fully understood and/or cannot be corrected for. This means that while the archaeological attestation of the presence of a species might generally be relied upon, it is highly unlikely that its absence is representative of true past distributions.

The alternative approach is to train the model using contemporary occurrence and environmental data and then use palaeoenvironmental data to ‘hindcast’ its predictions backwards in time. Like [Franklin et al. \(2015\)](#), we view the hindcast-

ing approach as more promising, because training datasets for both occurrences and environment are far more readily available, complete and reliable for the present than the past. There is some scepticism in the ecological niche modelling literature about the ability of such models to make accurate predictions in unknown environments (like the past) (?), but here the hindcasting approach also presents an opportunity: it reserves archaeological occurrence data as an independent dataset that can be used to assess the retrodictive performance of the model. This possibly was suggested by [Franklin et al. \(2015\)](#) but to our knowledge our study represents the first attempt to actually do so.

The major practical limitation of the hindcasting approach is that it relies on spatially explicit, high resolution palaeoenvironmental surfaces with continuous coverage of the region and periods of interest. Until recently, this has not been widely available for most applications, which is perhaps why only a minority of studies use it (cf. [Yaworsky et al., 2023](#)). In this study, we are able to take advantage of the increasing availability of high resolution, global palaeoclimate data derived from simulation experiments with general circulation models of climate ([Brown et al., 2018](#); ?; ?).

### 3. Methods and materials

We began by considering 62 distinct taxa (Table 1) - all the identifiable species known to be present at more than three Neolithic (c. 11.7–6.5 ka) sites in West Asia, according to our previous study of the regional archaeobotanical data ([Arranz-Otaegui and Roe, 2023](#)). Taxonomic names were resolved to the canonical form specified in the GBIF Backbone Taxonomy (?). So for example occurrences for *Bolboschoenus maritimus* also include those recorded under the older nomenclature *Scirpus maritimus* (see Table 1). Domestic species meeting our inclusion criteria were substituted with their wild progenitor(s), where different.

#### 3.1. Occurrence data

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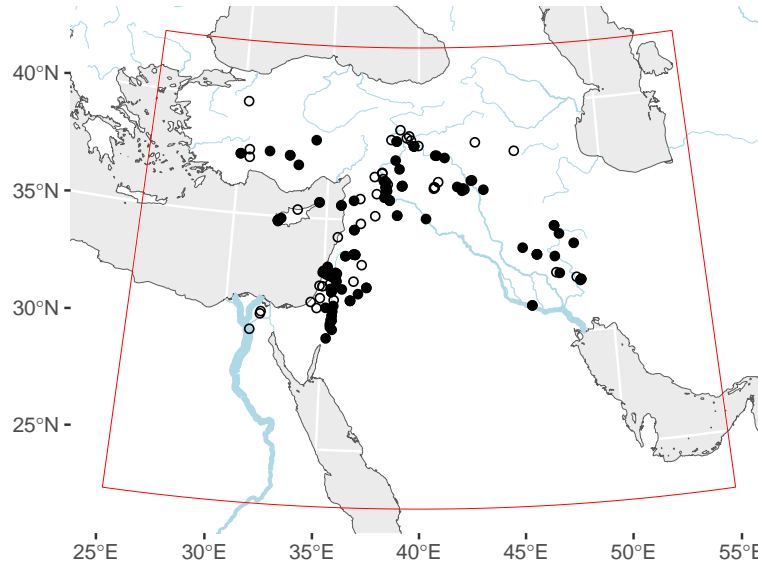


Figure 1: Study region (red) and archaeological sites used to generate modelled flora. Solid circles indicate Neolithic sites.

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Georeferenced occurrence data was obtained from the Global Biodiversity Information Facility (GBIF) using via its application programming interface and the R package ‘`rgbif`’ (Chamberlain and Boettiger, 2017; Chamberlain et al., 2024). GBIF occurrences marked as having imprecise or duplicate coordinates were excluded from the training dataset, as were fossil records. Although niche models have reasonable predictive power even with small training samples (Stockwell and Peterson, 2002; Hernandez et al., 2006; Wisz et al., 2008), we excluded 57 taxa with less than 50 occurrences in West Asia, following recommendations for niche models generally and Random Forest-based models specifically (Stockwell and Peterson, 2002; ?). We also excluded one taxon (*Avena sterilis*) with over 50,000 occurrences, as this would have been computationally prohibitive and we were uncertain what account for such a disproportionately high number of records.

Occurrence data only tells us where a species is present; there is rarely definitive information on where the species is *not* found. We therefore need to generate random background points or “pseudo-absences” to feed to the model. There are several ways to do this. We follow the advice of Barbet-Massin et al. (2012) for regression-based species distribution models and use a large (:10000) random sample of points, weighted equally against the presences in the regression. Valavi et al. (2022) also recommend using a very large background sample for random forest models.



Table 1: Recorded occurrence of flora considered in this study in Neolithic and contemporary West Asia

| Taxon   |
|---|
| <i>Triticum turgidum dicoccum</i> incl. <i>Triticum aestivum</i> , <i>Triticum dicoccoides</i> , <i>Triticum dicoccum</i> |
| <i>Hordeum spontaneum</i> incl. <i>Hordeum vulgare</i>  |
| <i>Triticum monococcum aegilopoides</i> incl. <i>Triticum boeoticum</i> , <i>Triticum monococcum</i>                      |
| <i>Bolboschoenus maritimus</i> incl. <i>Scirpus maritimus</i>   |
| <i>Vicia ervilia</i>  |
| <i>Buglossoides tenuiflora</i>  |
| <i>Arnebia decumbens</i>  |
| <i>Buglossoides arvensis</i>  |
| <i>Medicago radiata</i>   |
| <i>Androsace maxima</i>   |
| <i>Vicia orientalis</i> incl. <i>Lens culinaris</i>   |
| <i>Medicago astroites</i> incl. <i>Trigonella astroites</i>   |
| <i>Arnebia linearifolia</i>   |
| <i>Linum bienne</i> incl. <i>Linum usitatissimum</i>  |
| <i>Gypsophila vaccaria</i> incl. <i>Vaccaria pyramidata</i>   |
| <i>Carex divisa</i>   |
| <i>Ficus carica</i>   |
| <i>Lathyrus oleraceus</i> incl. <i>Pisum elatius</i> , <i>Pisum sativum</i>   |
| <i>Vicia faba</i>   |
| <i>Aizoanthemopsis hispanica</i> incl. <i>Aizoon hispanicum</i>   |
| <i>Bolboschoenus glaucus</i>  |
| <i>Pistacia atlantica</i>   |
| <i>Polygonum arenarium arenarium</i> <sup>9</sup> incl. <i>Polygonum venantianum</i>                                      |
| <i>Prosopis farcta</i>  |
| <i>Rumex pulcher</i>  |
| <i>Ammi majus</i>   |
| <i>Cicer reticulatum</i> incl. <i>Cicer arietinum</i>   |

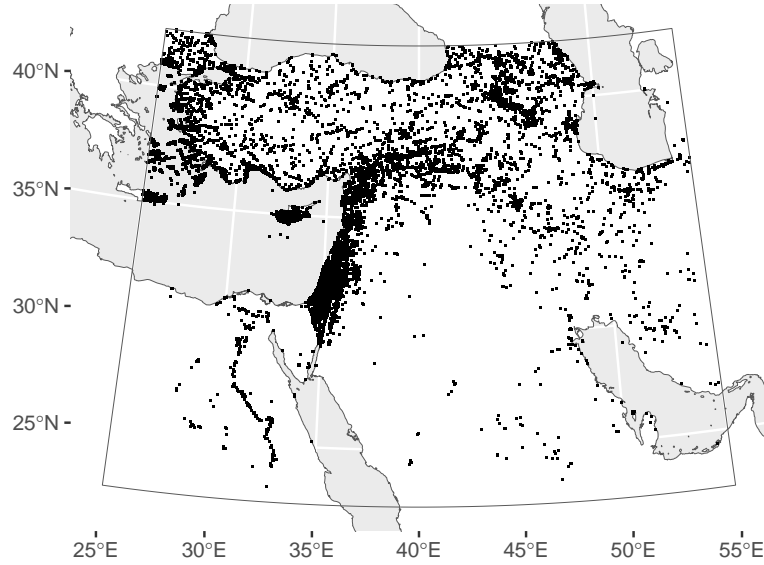


Figure 2: Georeferenced occurrence records from West Asia for the `r_nrow(flora)` modelled taxa ( $N=r\_nrow(unnest(flora, occ))$ )

### 3.2. Predictor data

We modelled the occurrence of species as a function of  $X$  spatial predictor variables (`?@tbl-predictors`). These included:

- Sixteen ‘bioclimatic’ variables derived from monthly temperature and precipitation values, following standard practice for species distribution models (Hijmans et al., 2005). Contemporary bioclimatic predictor data for West Asia was extracted from the global CHELSA dataset (Karger et al., 2017), which predicts temperature and precipitation from downscaled general circulation model output at 1 km resolution.
- Terrain aspect and slope, which at high resolution perform well as proxies for solar radiation when modelling plant occurrence (Austin and Van Niel, 2011; Leempoel et al., 2015); and the topographic wetness index (TWI), which serves as a proxy for soil moisture and is particularly important in modelling arid environments (Kopecký and Čížková, 2010; Campos et al.,

Table 2

| Period               | Age, ka   |
|----------------------|-----------|
| Bølling-Allerød (BA) | 14.7–12.9 |
| Younger Dryas (YDS)  | 12.9–11.7 |
| Early Holocene (EH)  | 11.7–8.3  |
| Current (CUR)        | —         |

Palaeoclimatic periods used for hindcasting, after [Brown et al.](#)

(2018)

[2016; Di Virgilio et al., 2018](#)). All three were derived from the SRTM15+ digital elevation model using algorithms from WhiteboxTools ([Lindsay, 2016](#)).

- Edaphic data from SoilGrids ([Hengl et al., 2014, 2017](#)), which improves model performance for plants ([Dubuis et al., 2013; Mod et al., 2016; Velazco et al., 2017](#)). Based on a recent assessment of the reliability of SoilGrids data for species distribution modelling ([Miller et al., 2024](#)), we used a subset of four variables relating to soil texture (clay, silt, sand) and pH at the surface (0-5 cm depth).

Predictor data was transformed to common equal-area projection and resolution of 5 km.

For hindcasting, we used reconstructed bioclimatic data for 3 key periods (Table 2) generated from downscaled paleoclimate simulations from the HadCM3 general circulation model ([Brown et al., 2018](#)). Terrain and soil predictors were held constant, since reconstructions of these variables in the past are not available at sufficient scale. It is not likely that either macroscale topography or soil characteristics have altered significantly over the period of time considered here, so we assume that this does not degrade model performance, and may in fact

benefit it by providing ‘anchoring’ predictors that are independent of climate change.

### 3.3. *Random Forest*

Ecological niche modelling is a classification problem that can be approached with a wide range of statistical methods. A substantial literature exists on the relative performance of these approaches and their respective parameterisations (reviewed in [Valavi et al., 2022](#)). Random Forest, a widely-used machine learning algorithm, is amongst the best performing methods for presence-only species distribution models, providing it is appropriately parameterised to account for the class imbalance between presence and background samples ([Valavi et al., 2021, 2022](#)). For our application, it also has the advantage of requiring little to no manual parameter tuning to achieve good predictive results, which makes it easier to model a larger numbers of taxa.

For each taxon we trained a classification model to predict occurrence (presence or absence/background) based on our X predictor variables (**?@tbl-predictors**). We used the Random Forest algorithm implemented in the R package ‘ranger’ ([Wright and Ziegler, 2017](#)) and the ‘tidymodels’ (?) framework for data preprocessing and model selection. To avoid overfitting, we follow [Valavi et al. \(2021\)](#) in their recommended hyperparameters and use of down-sampling to balance presence and background samples. Models for each taxon were fit independently, with redundant zero-variance predictors excluded, and assessed based on balanced training ( $\frac{3}{4}$ ) and test ( $\frac{1}{4}$ ) partitions.

## 4. Results

We trained Random Forest models for 56 taxa using contemporary occurrence data from GBIF, a random sample of background points, and the predictor variables described in **?@tbl-predictors**. Substituting the “current” climate predictors for those derived from palaeoclimatic simulations ([Brown et al., 2018](#)), we could then generate hindcast predictions for reconstructed past environments

in 4 key climate periods – a total of 224 modelled palaeodistributions. Predicted distributions for individual taxa are presented in the appendix and accompanying material.

#### 4.1. Model assessment

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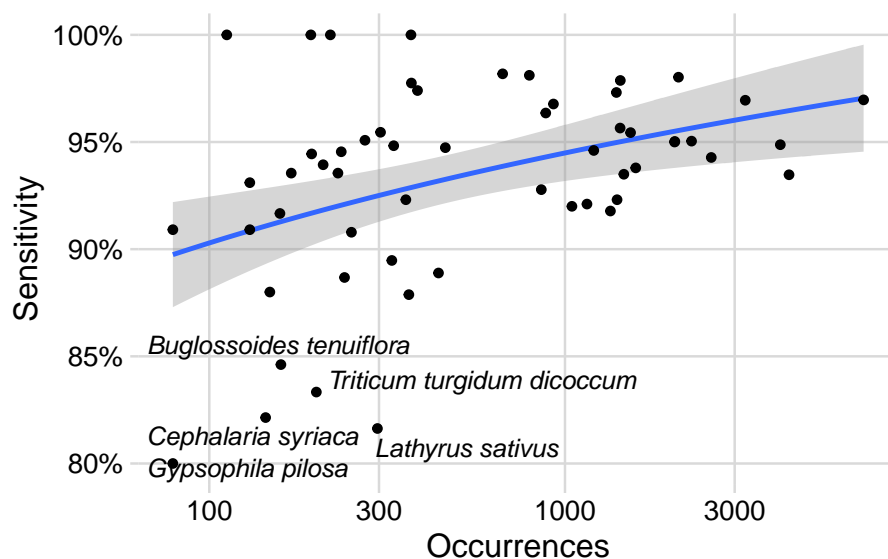


Figure 3: Number of taxon occurrences and model sensitivity on test dataset

We assessed the predictive performance of the fitted niche models in the contemporary environment based on the reserved test partition. Model accuracy (proportion of correctly classified presence and background samples) ranged between 72% and 98%, with an average of 91%. Sensitivity (proportion of correctly classified presence samples) ranged between 80% and 100%, with an average of 93%. The area under the models' receiver operating characteristic curves (ROC-AUC) was in the range of  $0.973 \pm 0.058$ . Model sensitivity is loosely correlated with the number of occurrences available for training (Figure 3), with the worst-performing models all having less than 300 recorded occurrences: *Buglossoides*

*tenuiflora*, *Cephalaria syriaca*, *Gypsophila pilosa*, *Lathyrus sativus*, and *Triticum turgidum dicoccum*. Test metrics and ROC curves for the individual models are included in the appendix.

The ability of the hindcast models to predict the occurrence of specific species at archaeological sites is significantly worse, with only 12% of presences in archaeobotanical assemblages successfully predicted.

## 5. Discussion

### 5.1. Reduction in range sizes over the Pleistocene/Holocene boundary

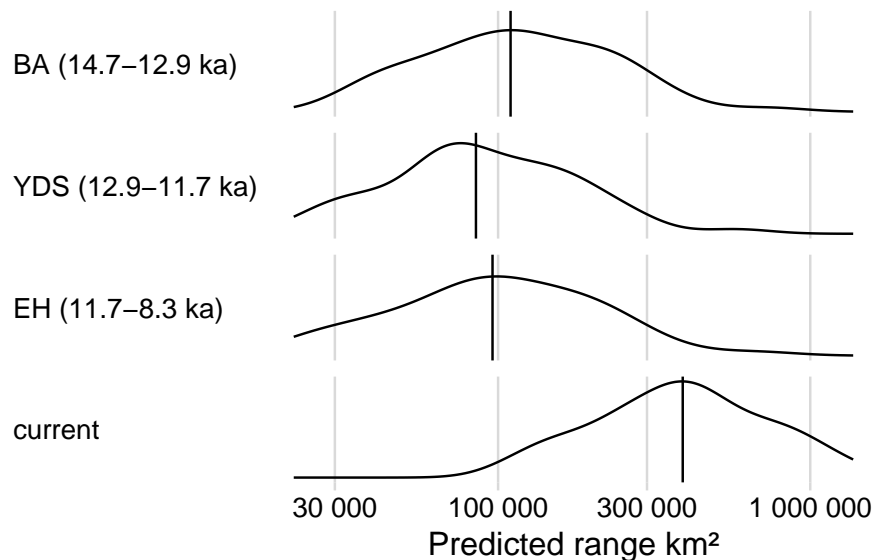


Figure 4: Distribution of predicted species ranges by period. Dashed lines indicate the median range.

Species ranges are predicted to have been significantly smaller in the terminal Pleistocene and Early Holocene than under current conditions Figure 4, though the magnitude of this change is likely also to reflect a degree of overfitting in the model (see below). Fluctuations in modelled range size between the Bølling-Allerød (14.7–12.9 ka), Younger Dryas (12.9–11.7 ka), and Early Holocene (11.7–8.3 ka) are more directly comparable. The average range of modelled species

shrank by 12% over the Pleistocene–Holocene boundary, with a noticeable dip in the Younger Dryas. This perhaps indicates that although this period is considered one of climatic amelioration globally (?), the colder conditions of the Pleistocene may have supported more extensive plant-based economies in West Asia specifically.

Many taxa that occur (or are predicted to occur) across the ‘hilly flanks’ today—including most crop progenitors—are reconstructed to have had a significantly more restricted distribution in the terminal Pleistocene/Early Holocene. These include *Ficus carica* (fig); *Hordeum* spp. (wild barleys); *Lathyrus aphaca* and *L. sativus* (both marginally edible legumes); *Triticum aestivum compactum* (in the N. Levant), *T. monococcum aegilopoides*, *T. durum*, and *Triticum urartu* (but not the other wheat progenitor, *T. turgidum dicoccum* – see below); *Aegilops speltoides*, but not *Aegilops tauschii* (goatgrasses); and *Vicia* spp. (vetches), including *Vicia faba* (broad beans). Central Anatolia, Northern Mesopotamia, and the Zagros Mountains in particular disappear from the predicted ranges of these species, leaving the Levant and to a lesser extent Western Anatolia Cyprus as refugia.

Our results for the Levant are consistent with the current understanding of this region as developing early intensive foraging economies [the Natufian culture, @] and as a centre of origin of agriculture [a]. It should also be noted that the selection of flora for this study (Table 1) is biased towards Levantine fauna due to the history of archaeological research in the region, as is the occurrence dataset used to train the model Figure 2. Within the Levant, retreat from the Badia.

Loss of the Northern Mesopotamia–Southeastern Anatolia region from the predicted ranges of crop progenitors is interesting in light of the ‘golden triangle’ hypothesis (?), which puts this region at the centre of the development of agriculture. Multiple lines of archaeological evidence have emerged that point away from this hypothesis and towards a more geographically diverse origin (??), but

it remains the area with some of the earliest clear evidence of domestication. Comparative genetics also points to the Northern Mesopotamia region as the centre of diversity of many crops (?). But since these studies are based on modern genomes, if the wild range of these plants has, as our modelling suggests, shifted since the Early Holocene, the apparent centre of diversity may have shifted with them. Our reconstructions are consistent with the late arrival of intensive plant-based foraging economies in this region (cf. the Natufian of the Levant) and more broadly there need not be a link between the core *wild* range of a plant and the core area of its domestication. A scenario in which cultivation emerged at the edges of the ranges of valuable plant resources—as a means of extend their natural niche—is also plausible.

The near-absence of the Zagros in any predicted ranges is also surprising, given mounting evidence that domestication took place just as early in the eastern *Mashriq* as it did in the west (???). We consider that the most likely explanation for this is that our flora does not include the species that were most important to plant subsistence in the east. Archaeobotanical data on Neolithic sites in the Zagros is limited (compared to the Levant in particular) due to a hiatus in field research there from the 1980s to early 2010s (?). Recent research (?) indicates ...

Cyprus and W. Anatolia not considered part of the core zone – maybe they should be?

Exceptions to the trend of range reduction include *Cicer reticulatum* (wild chickpea), which has a relatively stable range centered on Northern Mesopotamia; and *Triticum turgidum dicoccum* (wild emmer wheat), which is predicted to have two very restricted ranges centered around the Black Sea Coast of Anatolia and the Palmyra basin. In the latter case, neither of these areas are part of the predicted modern distribution of wild emmer (centered around the Caucasus and Northern Mesopotamia), but it would be consistent with archaeological evidence for early cultivation at Tell Abu Hureyra and



other sites in the Upper Euphrates. On the other hand, the model for *Triticum turgidum dicoccum* has the lowest predictive performance of all our fitted models.

### 5.2. Biogeography of crop progenitors

Several crop progenitors reduced in range before cultivation? Reduction in range from BA to EH very evident in *Hordeum*, *Pistacia atlantica*.

The wheat story.

Flax has a very restricted distribution (consistent with low occurrence in founders paper?). As does *Pistacia atlantica*, *Bolboschoenus maritimus*

*Secale cereale* = an Anatolian boy

### 5.3. Hindcast models do not predict archaeobotanical composition

The failure of our hindcast models to predict the occurrence of species in archaeobotanical assemblages has several possible explanations. Since they do accurately predict the test dataset, a likely culprit is overfitting of the models to the present environment. This implies that the modelled palaeodistributions should be seen as conservative estimates or a minimal range. Another obvious flaw in our methodology is that the time slices used for palaeoclimatic reconstruction are very broad—each covering around two millennia—and therefore potentially unrepresentative of the environment around sites at the specific time at which they were occupied. The variable quality of the archaeological test dataset, especially in terms of chronology, is also a plausible factor.

At the same time, we cannot rule out more substantive reasons for the discrepancy between predicted and observed archaeological occurrences. The niches of the modelled species could have changed since the Early Holocene, which would not be captured in a model trained purely on modern specimens. Human economic choices—mobility, foraging strategies, cultivation, etc.—could

also produce archaeobotanical assemblages whose composition depart significantly from that of the surrounding local flora. Further refinement of the methodology for hindcast palaeoecological niche models, for example using more finely resolved palaeoclimate sequences (e.g. ?), hyperparameter tuning to avoid overfitting, and improved archaeological datasets, would help disentangle these potential explanations.

## 6. Conclusion

- We present the first continuous, spatially explicit models of the palaeodistributions of 56 plant species found regularly in association with early agricultural archaeological sites in West Asia
  - A new line of evidence on archaeoecology
  - Complementary to archaeobot/pollen/etc. because it is independent from it
  - All models are wrong... but it's easier to see how these are wrong than lines on maps
- Modelling at scale using random forest, modern occurrences, and hindcasting represents a significant advance in pENM methodology
  - Relies on recent open ecological and climatic datasets
  - ...open archaeological datasets still lacking!
- First (? - check Yaworsky) attempt to verify hindcast models with archaeological compositional data
  - Results not too promising, but this doesn't mean the models are useless!
  - Discrepancies suggests several areas for further research and methodological development

## 7. References

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