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RESEARCH PAPER

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Pollen-derived biomes in the Eastern Mediterranean–Black Sea–Caspian-Corridor

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Abstract

Aim: To evaluate the biomization technique for reconstructing past vegetation in the Eastern Mediterranean–Black Sea–Caspian-Corridor using an extensive modern pollen data set and comparing reconstructions to potential vegetation and observed land cover data.

Location: The region between 28–48°N and 22–62°E.

Methods: We apply the biomization technique to 1,387 modern pollen samples, representing 1,107 entities, to reconstruct the distribution of 13 broad vegetation categories (biomes). We assess the results using estimates of potential natural vegetation from the European Vegetation Map and the Physico-Geographic Atlas of the World. We test whether anthropogenic disturbance affects reconstruction quality using land use information from the Global Land Cover data set.

Results: The biomization scheme successfully predicts the broadscale patterns of vegetation across the region, including changes with elevation. The technique discriminates deserts from shrublands, the prevalence of woodlands in moister lowland sites, and the presence of temperate and mixed forests at higher elevations. Quantitative assessment of the reconstructions is less satisfactory: the biome is predicted correctly at 44% of the sites in Europe and 33% of the sites overall. The low success rate is not a reflection of anthropogenic impacts: only 33% of the samples are correctly assigned after the removal of sites in anthropogenically altered environments. Open vegetation is less successfully predicted (33%) than forest types (73%), reflecting the under-representation of herbaceous taxa in pollen assemblages and the impact of long-distance pollen transport into open environments. Samples from small basins (<1 km^2) are more likely to be reconstructed accurately, with 58% of the sites in Europe and 66% of all sites correctly predicted, probably because they sample an appropriate pollen source area to reflect regional vegetation patterns in relatively heterogeneous landscapes. While methodological biases exist, the low confidence of the quantitative comparisons should not be over-emphasized because the target maps themselves are not accurate representations of vegetation patterns in this region.

Main Conclusions: The biomization scheme yields reasonable reconstructions of the broadscale vegetation patterns in the Eastern Mediterranean–Black Sea–Caspian-Corridor, particularly if appropriate-sized sampling sites are used. Our results indicate biomization could be used to reconstruct changing patterns of vegetation in response to past climate changes in this region.

KEYWORDS
biomization, Black Sea region, Eastern Mediterranean, human impact, land cover, palaeoclimate, surface pollen samples, vegetation change

1 | INTRODUCTION

The reconstruction of changes in regional vegetation patterns from pollen data during the geologic past is important for several reasons. These reconstructions can provide insights into the response of vegetation to climate changes (Harrison & Prentice, 2003; Harrison & Sanchez Goni, 2010) and human activities (Cui et al., 2014; Gaillard, Sugita, Bunting, Dearing, & Bittman, 2008). They are a tool to explore the interactions between changes in natural resources and human cultures (e.g. Connor et al., 2013) and can also be used to test climate model simulations (e.g. Wohlfahrt et al., 2008), and as inputs for such simulations (e.g. Swann, Fung, Liu, & Chiang, 2014).

There are several approaches to reconstruct past vegetation patterns from pollen data in an objective way (see e.g. Binney et al., 2017; Fyfe, Roberts, & Woodbridge, 2010; Gachet et al., 2003; Hellman, Gaillard, Broström, & Sugita, 2008; Prentice, Guiot, Huntley, Jolly, & Cheddadi, 1996; Sugita, 2007). All of these techniques utilize modern pollen–vegetation relationships as a basis for interpreting past records yet they differ in the degree to which they rely chiefly on indicator taxa or group taxa into functional types, the type and amount of vegetation information used in the calibration, and the complexity of the model used to link pollen to vegetation types. One of the simplest methods, and the only one to have been applied globally, is biomization (Prentice & Jolly, 2000; Prentice et al., 1996). The biomization technique classifies the taxa present in pollen assemblages into a small number of plant functional types (PFTs); major terrestrial vegetation types (biomes) are defined by a characteristic association of PFTs based on knowledge of the regional vegetation. The process of classification is iterative to allow for uncertainties in both taxa to PFT and PFT to biome assignment and to mitigate problems of pollen representation. However, the iterative nature of the biomization procedure means that it is important to test the method for each individual region.

Applications of the biomization technique in specific regions have identified a number of potential problems that can affect the reliability of the reconstructions. These include (1) the ambiguity of assignments of pollen taxa to PFTs, (2) pollen production biases which generally result in the over-representation of woody species and the under-representation of herbaceous species in the pollen assemblage, (3) difficulties in selecting sites that adequately represent pollen source area in areas characterized by fine-scale heterogeneity in vegetation patterns, (4) transport of tree pollen into non-forested areas resulting in poor delineation of ecotonal boundaries, (5) upslope transport of pollen from lowland areas in mountainous areas resulting in poor delineation of altitudinal vegetation gradients and tree line, and (6) human disturbance or alteration of vegetation, particularly in regions with a long history of cultivation, which can result in poor representation of modern vegetation patterns in modern pollen surface samples. These various issues have been offered as post hoc explanations for mismatches between expected and actual reconstructions, based on a general understanding of pollen–vegetation relationships and were not explicitly tested in the regional applications of the biomization technique.

The region linking the Middle East and Eastern Europe, here referred to as the Eastern Mediterranean–Black Sea–Caspian-Corridor (28–48°N and 22–62°E), is an ideal region to test the impact of these potential problems on biome reconstructions. It is characterized by strong temperature and precipitation gradients as well as topographic diversity. Regional climates range from temperate continental in the north-west of the region to summer-dry Mediterranean and humid warm-temperate (Euxinian, Hyrcanian) in the south and south-east. East of the Caucasus Mountains and south of the Pontic, Taurus and Alborz Mountains, aridity increases and deserts occur. There is a great diversity of vegetation types in the region (Figure 1), including montane grasslands and shrub-tundra, cool needle-leaved or mixed forest communities dominated by fir, spruce, cedar and beech in the mountain areas, a large variety of oak-dominated woodlands in the lower mountain belts and plains (including evergreen species in the Mediterranean climate zone), small areas of humid malacophyll forest, and vast areas dominated by steppe, shrubland and sparse desert vegetation (Zohary, 1973). Superimposed on the broad regional vegetation gradients, topographic diversity produces heterogeneous and fine-scaled vegetation patterning. Furthermore, this is a region that has been at the crossroads of the spread of human populations and cultural exchange between Europe and Asia in both modern and prehistoric times (Connor et al., 2013; Dolukhanov & Arslanov, 2007; Müller et al., 2011; Turney & Brown, 2007). Thus, it also provides an ideal test case for the impact of human activities on vegetation and on our ability to reconstruct natural vegetation patterns from pollen.

The availability of reliable potential vegetation maps has posed problems for the quantitative evaluation of previous regional biomizations. In many cases, biome reconstructions were evaluated solely against the plausibility of the mapped geographic and altitudinal patterns in vegetation distribution compared to field knowledge (e.g. Prentice et al., 1996; Tarasov et al., 1998), against model-simulated vegetation patterns (e.g. Yu et al., 2000) or using simplified maps constructed from multiple sources (e.g. Bigelow et al., 2003; Marchant et al., 2009; Takahara et al., 2000). Here again, the Eastern Mediterranean–Black Sea–Caspian-Corridor provides a useful test case because there are potential vegetation maps for large parts of the region (Bohn et al., 2003; Gerassimov, 1964). Furthermore, there is now information on land use derived from remotely sensed data (Hartley et al., 2006; Tateishi, Zhu, & Sato, 2003), which provides an opportunity to explicitly test whether anthropogenic alteration of the landscape has a major impact on the ability to reconstruct potential vegetation patterns.

Although a few sites from the Eastern Mediterranean–Black Sea–Caspian-Corridor region were included in previous regional biomizations (e.g. Elenga et al., 2000; Prentice et al., 1996; Tarasov et al., 1998, 2000), there has been no systematic application and evaluation of biomization techniques across the region. In this study, we use modern data from an expanded version of the EMBSeCBIO database (Cordova et al., 2009) to evaluate how well potential natural vegetation and current vegetation types are reflected in pollen assemblages in the Eastern Mediterranean–Black Sea–Caspian-Corridor, using both qualitative and quantitative comparisons of the vegetation reconstructions obtained through biomization with vegetation maps. We explicitly test the impact of potential problems such as site selection and human impact on the reliability of the reconstructions and provide recommendations on the most robust way to use biomization to reconstruct vegetation changes in heterogeneous landscapes.

2 | MATERIALS AND METHODS

2.1 | Pollen records

Pollen data were contributed by members of the Eastern Mediterranean–Black Sea–Caspian Biomes (EMBSeCBIO) project (Cordova et al., 2009); this includes unpublished data from the current authors. This was supplemented by data from the BIOME 6000 database (Bigelow et al., 2003; Prentice & Jolly, 2000), the European

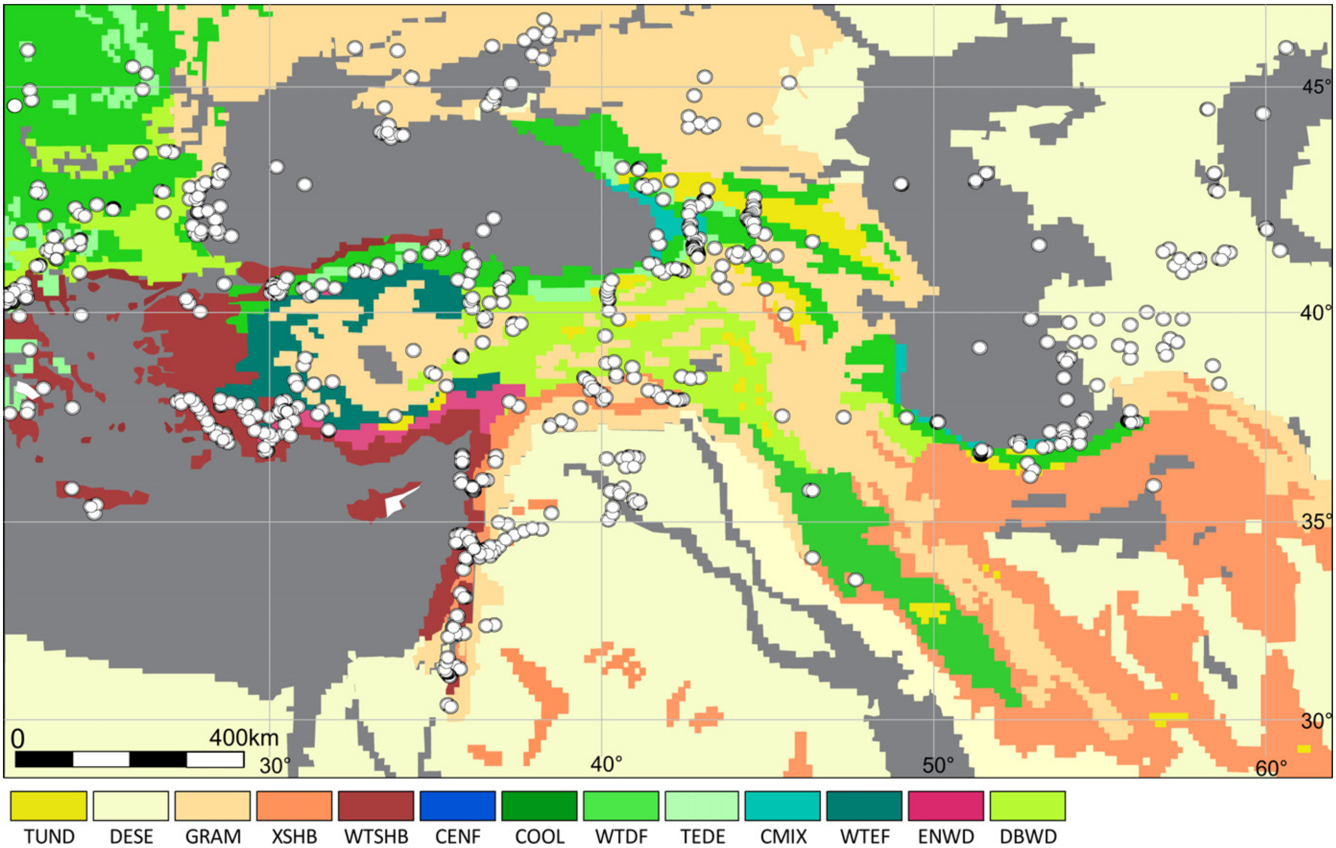

FIGURE 1 Map of the study area showing the distribution of major biomes as defined for the Eastern Mediterranean–Black Sea–Caspian biomization. The biome codes are TUND: tundra, DESE: desert, GRAM: graminoids with forbs, XSHB: xeric shrubland, WTSHB: warm-temperate evergreen sclerophyll broadleaf shrubland, CENF: cold evergreen needleleaf forest, COOL: cool evergreen needleleaf forest, WTDF: warm-temperate deciduous malacophyll broadleaf forest, TEDE: temperate deciduous malacophyll broadleaf forest, CMIX: cool mixed evergreen needleleaf and deciduous broadleaf forest, WTEF: warm-temperate evergreen needleleaf and sclerophyll broadleaf forest, ENWD: evergreen needleleaf woodland, and DBWD: deciduous broadleaf woodland. The distribution of modern pollen samples used is also shown by dots

Pollen Database (Fyfe et al., 2009), the European Modern Pollen Database (Davis et al., 2013) and the Global Pollen Database (http://www.ncdc.noaa.gov/paleo/gpd.html). The final data set provides unsurpassed coverage of the region in terms of pollen sites (see Figure 1; Appendix S1).

The structure and contents of the EMBSeCBIO database are described in Cordova et al. (2009). The radiocarbon ages of the pollen records were calibrated with the OxCal software package (Bronk Ramsey, 2009). Marine reservoir ages were calculated using the Marine 09 calibration curve with the appropriate regional Δ*R* for different regions of the Black and Marmara Seas. A "modern" pollen data set was extracted from the database, where modern was defined as younger than 250 calibrated years before present (cal BP). In cases where multiple samples occurred within this 250-year window, we used the youngest sample. The data set was filtered to remove samples with low taxonomic resolution (i.e. where most taxa were only identified to family level), poor sample preservation (indicated by samples with a predominance of a single taxon) and samples from locations heavily influenced by local wetland taxa. The data set consists of 1,387 samples, of which 193 samples come from the upper part of a lake, bog or other type of sediment core, 45 samples from marine cores and 28 samples from sediment profiles. A single pollen trap record was used; these data were averaged over a 5-year period.

2.2 | Biomization

The biomization procedure (Prentice et al., 1996) classifies the taxa present in pollen assemblages into a small number of plant functional types (PFTs) and subsequently into major terrestrial vegetation types (biomes). The biome scheme used in this study represents the 13 major biomes in the study region (Figure 2). Each of these biomes is defined by a unique combination of PFTs (Table 1). Many PFTs occur in more than one biome; the PFT differentiating one biome from another is not required to be the dominant or most abundant life-form.

More than 1,000 pollen taxa are represented in the modern data set. Aquatic and exotic taxa, and taxa representing cultivars, were excluded from the data matrix, because the aim was to produce reconstructions of natural regional vegetation patterns. The remaining 698 pollen taxa were assigned to PFTs based on field knowledge of the regional vegetation, guided by the allocations given by Bigelow et al. (2003), Elenga et al. (2000), Prentice et al. (1996), Tarasov et al. (2000) and by reference to the literature (Davis, 1965-1988;

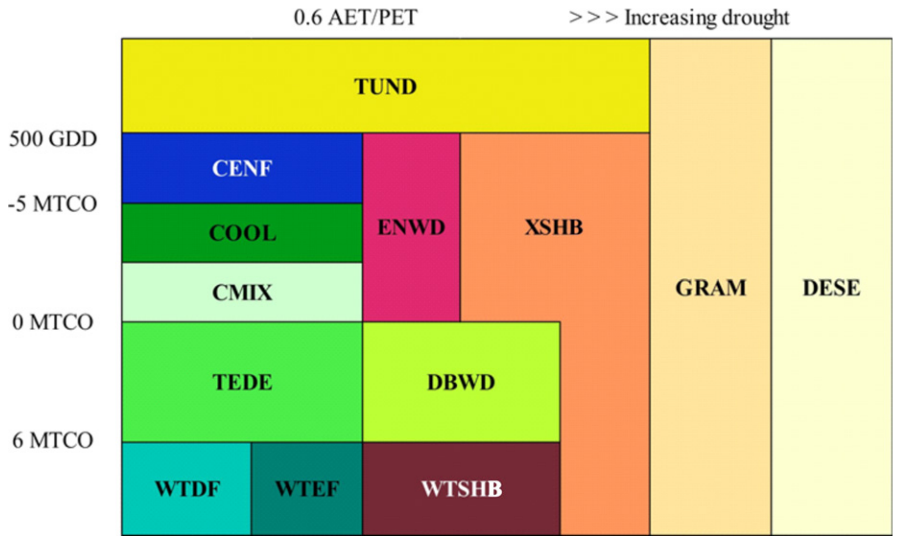

FIGURE 2 Conceptual model of the distribution of the 13 biomes recognized in the Eastern Mediterranean–Black Sea–Caspian biomization in climate space. MTCO: mean temperature of the coldest month, GDD: growing degree days, AET/PET: actual evapotranspiration/potential evapotranspiration. The biome codes are TUND: tundra, DESE: desert, GRAM: graminoids with forbs, XSHB: xeric shrubland, WTSHB: warm-temperate evergreen sclerophyll broadleaf shrubland, CENF: cold evergreen needleleaf forest, COOL: cool evergreen needleleaf forest, WTDF: warm-temperate deciduous malacophyll broadleaf forest, TEDE: temperate deciduous malacophyll broadleaf forest, CMIX: cool mixed evergreen needleleaf and deciduous broadleaf forest, WTEF: warm-temperate evergreen needleleaf and sclerophyll broadleaf forest, ENWD: evergreen needleleaf woodland, and DBWD: deciduous broadleaf woodland

Tutin et al., 1964-1980). Some pollen taxa, especially those representing higher taxonomic categories (e.g. Asteraceae) or with a broad ecological range (e.g. *Pinus*, *Quercus*), were assigned to more than one PFT. The presence of generalist taxa, or more specialist taxa that are over-represented in the pollen sum, may make it difficult to distinguish some biomes. This is dealt with by allocating them only to PFTs for which they are diagnostic (rather than characteristic) in an iterative fashion. Thus, the final allocation of taxa to PFTs (Table 2) reflects both botanical information and the importance of a taxon to the PFT within the EMBSeCBIO region.

Affinity scores between each pollen spectrum and each biome are calculated as the sum of pollen percentages for the taxa in the PFTs that may occur in that biome. Prior to this calculation, the pollen values are adjusted by square root transformation to increase the signal-to-noise ratio and correct for the over-representation of taxa that produce large quantities of pollen (Prentice et al., 1996). The minimum threshold for inclusion of a taxon is 0.5%. Each pollen spectrum was assigned to the biome to which it has the highest affinity score. Some biomes are characterized by a subset of the PFTs present in another biome (e.g. the PFTs defining deciduous forest types are often a subset of those defining equivalent mixed forest types); such biomes could have identical affinity scores. When equal affinity scores were obtained for more than one biome, biomes were assigned in the order shown in Table 1.

2.3 | Evaluation

Biome reconstructions can be evaluated based on the plausibility of the mapped geographic and altitudinal patterns in vegetation distribution compared to field knowledge (e.g. Prentice et al., 1996). Nevertheless, it is also helpful to make quantitative evaluations using a matrix of predicted versus observed vegetation at each site (see e.g. Bigelow et al., 2003). In the absence of information on the vegetation at the pollen sites, we used vegetation maps to provide evaluation targets. There is no single source of vegetation data for this region. The *Physico-Geographic Atlas of the World* (FGAM: Gerassimov, 1964) provides information on potential natural vegetation patterns at a scale of 1:10,000,000 for Europe and 1:25,000,000 for Asia. FGAM was constructed by combining information on climate, soils, aspect and relief with data on plant distribution and the presence of relict vegetation. The European Vegetation Map (EVM: Bohn et al., 2003) uses a similar approach but provides more detailed information on potential vegetation for the European part of the study area (scale 1:2,500,000).

We translated the vegetation descriptions given in FGAM and EVM into the EMBSeCBIO biomes for comparison with the pollen-based reconstructions. Unfortunately, even at the aggregated level of biomes, the agreement between the two maps in the region covered by both is poor: only 33% of the 444 sites covered by both EVM and FGAM were classified as the same biome. The poor agreement between the two maps casts doubt on their reliability; nevertheless, quantitative evaluation can provide insights about potential sources of bias. As EVM is based on more extensive field mapping, our target data set was based on the EVM data when available and FGAM for other sites (Appendix S2). We also examined the degree of coherence between reconstructed and observed biomes based solely on the subset of sites covered by the EVM.

The modern landscape has been affected by human activities and this could make it difficult to reconstruct potential vegetation from modern pollen. The Global Land Cover data set (GLC2000:

TABLE 1 Assignment of plant functional types (PFTs) to biomes used in the Eastern Mediterranean–Black Sea–Caspian region. The order of the biomes reflects the order used in the tie-break procedure

	Biome	Biome code	Constituent plant functional types
1	Tundra	TUND	Arctic forb, sedge graminoid, arctic dwarf shrub, arctic low-to-high shrub
2	Desert	DESE	Halophyte, rosette or cushion forb, succulent, switch plant, tuft tree
3	Graminoids with forbs	GRAM	Grass graminoid, geophyte, other forb
4	Xeric shrubland	XSHB	Drought-tolerant forb, switch plant, xerophytic shrub
5	Warm-temperate evergreen sclerophyll broadleaf shrubland	WTSHB	Warm-temperate low-to-high shrub, temperate low-to-high shrub, warm-temperate sclerophyll tree
6	Cold evergreen needleleaf forest	CENF	Boreal low-to-high shrub, boreal cold-deciduous malacophyll broadleaved tree, boreal evergreen needle-leaved tree, boreal needle-leaved deciduous tree, eurythermic evergreen needle-leaved tree
7	Cool evergreen needleleaf forest	COOL	Boreal cold-deciduous malacophyll broadleaved tree, boreal evergreen needle-leaved tree, cool-temperate evergreen needle-leaved tree, temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree, temperate evergreen needle-leaved tree
8	Warm-temperate deciduous malacophyll broadleaf forest	WTDF	Temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree, temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree, warm-temperate sclerophyll tree, climber/liana/vine
9	Temperate deciduous malacophyll broadleaf forest	TEDE	Temperate (frost-induced late budburst) cold-deciduous malacophyll broadleaved tree, temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree, temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree, eurythermic evergreen needle-leaved tree, climber/liana/vine
10	Cool mixed evergreen needleleaf and deciduous broadleaf forest	CMIX	Cool-temperate evergreen needle-leaved tree, eurythermic evergreen needle-leaved tree, temperate (frost-induced late budburst) cold-deciduous malacophyll broadleaved tree, temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree, temperate evergreen needle-leaved tree
11	Warm-temperate evergreen needleleaf and sclerophyll broadleaf forest	WTEF	Warm-temperate needle-leaved evergreen tree, warm-temperate sclerophyll tree, warm-temperate evergreen malacophyll broadleaved tree, temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree, eurythermic evergreen needle-leaved tree
12	Evergreen needleleaf woodland	ENWD	Warm-temperate low-to-high shrub, other forb, eurythermic evergreen needle-leaved tree, warm-temperate needle-leaved evergreen tree
13	Deciduous broadleaf woodland	DBWD	Warm-temperate evergreen malacophyll broadleaved tree, temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree, warm-temperate low-to-high shrub, temperate low-to-high shrub, other forb

Hartley et al., 2006; Tateishi et al., 2003) documents land cover in 2,000 AD at 1 km resolution, using 22 land cover classes for Europe and 31 classes for Asia. There is no direct translation of the GLC2000 natural vegetation classes to the EMBSeCBIO biomes: some GLC2000 classes correspond to several biomes. Thus, we only use GLC2000 to assess the impact of anthropogenic land use on the quality of our reconstructions by excluding pollen sites that fall within the GLC2000 land use classes artificial surfaces and associated areas, cultivated and managed areas, irrigated agriculture, and mosaics including croplands (Appendix S2) from our quantitative comparisons. There are data gaps in some parts of Asia, so the GLC2000 data set could not be used to evaluate reconstructions from the region between 30–32° N and 47–48° E.

3 | RESULTS

The biomization procedure captures the large-scale geographic patterns of vegetation distribution across the region (Figures 3 and 4). It correctly predicts the distribution of forests in the Eastern Mediterranean, on the coastal plains around the Mediterranean, to the south of the Black and Caspian Seas. It also correctly predicts forests in mountainous areas in the Balkans, Turkey and in the Caucasus (Figures 3 and 4). It captures the transition to shrubland at lower elevations, giving way to more xeric vegetation and deserts to the north of the Black Sea, east of the Caspian Sea, and in inland regions of the Middle East.

The quantitative evaluation of the biome reconstructions is less satisfactory. Only 33% of the 1,181 sites for which comparisons are possible are correctly predicted when compared to the composite EVM/FGAM data set (Table 3). However, this increases to 44% for the 589 sites where direct comparison with the EVM data set is possible (Table 4). Sample type affects the accuracy of the reconstruction: 35% of surface samples (moss polsters, soil samples, surface sediments) compared to 25% of core/section samples are correctly assigned when compared to the composite EVM/FGAM data set. Samples from small basins (<1 km^2) are more likely to be predicted correctly than samples from large basins, with 62% of the sites in Europe and 58% of all sites correctly predicted (Table 5). This improvement in prediction probably reflects the fact that small

TABLE 2 Assignment of pollen taxa to plant functional types (PFTs) used in the Eastern Mediterranean–Black Sea–Caspian-Corridor biomization

Plant functional type	Constituent taxa
Arctic forb	*Aconitum*, *Aconitum* type, *Androsace*, *Anemone*, *Anemone nemorosa* type, *Anemone* type, *Aquilegia* type, Campanulaceae, *Cardamine*, *Drosera*, *Gentiana*, *Gentiana nivalis* type, *Gentiana pneumonanthe* type, Gentianaceae, *Gentianella campestris* type, Herbs, *Jasione*, *Parnassia*, *Parnassia palustris*, *Phyteuma*, *Phyteuma* type, *Pinguicula*, Polygonaceae, *Polygonum*, *Polygonum* type, *Pulsatilla*, Ranunculaceae, *Rosa*, *Rosa* type, *Sagina*, *Saussurea*, *Saxifraga*, *Saxifraga hirsuta* type, *Saxifraga nivalis* type, *Saxifraga oppositifolia*, *Saxifraga oppositifolia* type, *Saxifraga rosacea*, *Saxifraga stellaris* type, Saxifragaceae, Scrophulariaceae, *Thalictrum*, *Thalictrum aquilegifolium*, *Trollius*, *Valeriana*, Valerianaceae, *Veratrum* type
Rosette or cushion forb	*Artemisia*, *Artemisia herba-alba* type, *Artemisia* type, Asteraceae, Asteraceae (Liguliflorae), Asteraceae (Tubuliflorae), *Astragalus*, *Astragalus* type, Crassulaceae, *Euphorbia*, *Gundelia* type, Herbs, *Marrubium*, *Phlomis*, *Scabiosa*, *Scabiosa columbaria* type, *Scleranthus*, *Scleranthus* type, *Tribulus*, *Zygophyllum*
Drought-tolerant forb	*Achillea*, *Achillea* type, *Adonis*, *Adonis aestivalis* type, *Adonis* type, Amaranthaceae/Chenopodiaceae, *Ambrosia*, *Ambrosia* type, *Armeria*, *Armeria/Limonium*, *Artemisia*, *Artemisia* type, *Artemisia vulgaris* type, *Aster*, *Aster* type, *Aster/Achillea*, *Aster/Achillea* type, Asteraceae, Asteraceae (Liguliflorae), Asteraceae (Tubuliflorae), *Astragalus*, *Astragalus* type, *Astrantia* type, *Atriplex*, Cannabaceae, *Cannabis*, *Cannabis sativa*, *Carduus*, *Carduus* type, *Carthamus*, Caryophyllaceae, *Centaurea*, *Centaurea cyanus*, *Centaurea cyanus* type, *Centaurea depressa*, *Centaurea depressa* type, *Centaurea jacea*, *Centaurea jacea* type, *Centaurea nigra* type, *Centaurea scabiosa*, *Centaurea scabiosa* type, *Centaurea solstitialis* type, Chenopodiaceae, Dipsacaceae, *Dipsacus*, *Dipsacus* type, *Echinops*, *Eryngium* type, *Euphorbia*, *Fagopyrum*, *Fagopyrum esculentum*, *Fagopyrum tataricum*, *Glaucium*, *Gundelia* type, *Gypsophila*, *Gypsophila* type, *Helichrysum*, *Heliotropium* type, Herbs, *Herniaria* type, *Hornungia* type, *Jurinea*, *Jurinea* type, *Knautia*, *Knautia arvensis*, *Limonium*, *Noaea* type, *Salvia*, *Scabiosa*, *Scabiosa columbaria* type, *Scabiosa rotata* type, Scrophulariaceae, *Serratula*, *Seseli libanotis* type, *Sideritis*, *Succisa*, *Thymus*, *Verbascum*, *Verbascum* type
Other forb	*Acanthus*, *Achillea*, *Achillea* type, *Aconitum*, *Aconitum* type, *Adoxa* type, *Agrimonia*, *Agrimonia eupatoria*, *Agrostemma* type, *Alchemilla*, Amaranthaceae/Chenopodiaceae, *Ambrosia*, *Ambrosia* type, *Ammi* type, *Anagallis*, *Anemone*, *Anemone* type, *Anthemis* type, *Anthriscus* type, Apiaceae, *Apium* type, *Arctium*, *Arctium/Jurinea*, *Asperula* type, *Aster*, *Aster* type, *Aster/Achillea*, *Aster/Achillea* type, Asteraceae, Asteraceae (Liguliflorae), Asteraceae (Tubuliflorae), *Bellis* type, *Beta*, *Bidens* type, Boraginaceae, *Brassica* type, Brassicaceae, Brassicaceae type, *Bunium* type, *Bupleurum*, *Bupleurum* type, *Caltha*, *Caltha* type, *Campanula*, *Campanula* type, Campanulaceae, Cannabaceae, *Capsella* type, *Carduus*, *Carduus* type, Caryophyllaceae, *Centaurea*, *Centranthus*, *Cerastium* type, *Chaerophyllum* type, *Cheilanthes*, *Chelidonium*, Chenopodiaceae, *Chrysosplenium*, *Chrysosplenium* type, Cichoriaceae, *Circaea*, *Cirsium*, *Cirsium* type, *Cirsium/Carduus*, *Cirsium/Gundelia*, *Conium maculatum*, *Consolida*, Convolvulaceae, *Convolvulus*, *Daucus* type, *Delphinium*, *Delphinium* type, *Dianthus*, *Dianthus* type, *Digitalis*, *Digitalis purpurea* type, *Diphasium alpinum* type, Dipsacaceae, *Dipsacus*, *Dipsacus* type, *Echium*, *Echium* type, *Echium violaceum*, *Epilobium*, *Epilobium* type, *Erodium*, *Euphrasia*, *Falcaria* type, *Ferula*, *Ferula* type, *Filago* type, *Filifolium sibiricum*, *Filipendula*, *Flammula* type, *Fragaria* type, *Fumaria*, *Galium*, *Galium* type, Geraniaceae, *Geranium*, *Geum*, *Geum* type, *Gnaphalium*, *Hedysarum* type, *Helleborus*, *Heracleum*, *Heracleum* type, *Hippocrepis* type, *Hyoscyamus*, *Hypericum*, *Hypericum assyriacum* type, *Hypericum hyssopifolium*, *Hypericum perforatum* type, *Hypericum* type, *Impatiens*, *Lactuca*, *Lathyrus*, *Lathyrus* type, *Legousia*, Leguminosae, *Lepidium*, *Lepidium* type, Linaceae, *Linaria*, *Linum*, *Linum* type, *Lithospermum*, *Lotus* type, *Lychnis* type, *Lysimachia*, *Malabaila*, *Malabaila* type, *Malva*, Malvaceae, *Matricaria* type, *Matthiola*, *Medicago*, *Melampyrum*, *Mercurialis*, *Mercurialis annua*, *Mercurialis perennis*, *Myosotis*, *Myosotis* type, *Nigella*, Onagraceae, *Onobrychis*, *Onobrychis* type, *Onosma*, *Origanum vulgare*, *Oxalis*, *Oxyria*, *Oxyria/Rumex*, *Papaver*, *Papaver rhoeas* type, Papaveraceae, *Parietaria*, *Paronychia*, *Paronychia/Polycnemum*, *Peucedanum* type, *Pimpinella*, *Pimpinella anisum* type, *Pimpinella major* type, *Pimpinella* type, Plantaginaceae, *Plantago*, *Plantago coronopus*, *Plantago coronopus* type, *Plantago lanceolata*, *Plantago lanceolata* type, *Plantago major*, *Plantago major* type, *Plantago major/Plantago media*, *Plantago maritima*, *Plantago maritima* type, *Plantago media*, *Plantago media* type, *Plantago ovate*, *Plantago ovata* type, Plumbaginaceae, Polemoniaceae, *Polemonium*, *Polygala*, Polygonaceae, *Polygonum*, *Polygonum* type, Portulacaceae, *Potentilla*, *Potentilla* type, *Primula*, Primulaceae, *Prunella* type, *Pulmonaria* type, Ranunculaceae, *Reseda*, Resedaceae, *Rhinanthus*, *Rhinanthus* type, *Rumex*, *Rumex acetosa*, *Rumex acetosa* type, *Rumex acetosa/Rumex acetosella*, *Rumex acetosella*, *Rumex acetosella* type, *Rumex cyprius*, *Rumex hydrolapathum*, *Rumex hydrolapathum* type, *Rumex patentia*, *Rumex patentia* type, *Rumex scutatus* type, *Rumex* type, *Sagina*, Salvia, *Sanguisorba*, *Sanguisorba minor*, *Sanguisorba minor* type, *Sanguisorba officinalis*, *Sanguisorba* type, *Sanicula* type, Scrophulariaceae, *Scutellaria*, *Senecio*, *Senecio* type, *Silene*, *Silene dioica* type, *Silene* type, *Silene vulgaris* type, *Sinapis* type, Solanaceae, *Solanum*, *Solanum nigrum*, *Spergula*, *Spergula arvensis*, *Spergula* type, *Spergula/Spergularia*, *Spergularia* type, *Stachys*, *Stachys* type, *Stellaria*, *Symphytum*, *Symphytum* type, *Taraxacum*, *Taraxacum* type, *Teucrium*, *Thesium*, *Torilis arvensis* type, *Torilis japonica* type, *Trifolium*, *Trifolium alpestre* type, *Trifolium pratense*, *Trifolium pratense* type, *Trifolium* type, *Turgenia* type, *Urtica*, *Urtica dioica*, *Urtica dioica* type, *Urtica pilulifera* type, *Urtica* type, Urticaceae, *Vaccaria* type, *Valeriana*, Valerianaceae, *Verbascum*, *Verbascum* type, *Verbena*, *Veronica* type, *Vicia*, *Vicia* type, *Viola*, Violaceae, *Xanthium*

(Continues)

TABLE 2 (Continued)

Plant functional type	Constituent taxa
Halophyte	Amaranthaceae/Chenopodiaceae, *Atriplex*, *Calligonum*, *Ceratoides*, Chenopodiaceae, *Crambe*, *Frankenia*, *Frankenia hirsute*, *Halogeton*, *Halothamnus* type, *Hammada* type, *Lycium*, *Nitraria*, *Peganum*, *Peganum harmala*, *Salsola*, *Salsola* type, *Suaeda*, *Suaeda* type, *Tamarix*
Geophyte	*Allium*, *Allium* type, *Anthericum* type, Araceae, *Asparagus* type, *Asphodeline*, *Asphodelus*, *Calamus*, *Colchicum*, *Cyclamen*, *Eremurus*, *Fritillaria* type, Iridaceae, *Iris*, Liliaceae, *Lilium*, *Maianthemum* type, *Muscari*, *Narthecium* type, *Ornithogalum* type, *Scilla* type, *Scorzonera*, *Scorzonera humilis* type, *Scorzonera* type, *Tulipa sylvestris* type, *Tulipa systola* type
Succulent	*Aellenia* type, Amaranthaceae/Chenopodiaceae, Chenopodiaceae, Crassulaceae, *Euphorbia*, *Sedum*, *Sedum* type, *Zygophyllum*
Grass graminoid	*Glyceria* type, *Lygeum*, Poaceae, *Secale*, *Secale* type, *Stipa*
Sedge graminoid	*Carex*, *Carex* type, *Cladium*, *Cladium mariscus*, Cyperaceae, *Cyperus*, *Fimbristylis*, Juncaceae, *Juncus/Luzula*, *Rhynchospora* type, *Scheuchzeria palustris*, *Schoenoplectus*
Arctic dwarf shrub	*Betula*, *Bruckenthalia*, *Dryas* type, Ericaceae, Ericaceae type, *Potentilla*, *Potentilla* type, *Primula*, Primulaceae, *Rheum*, *Rheum* type, *Rubus arcticus*, *Rubus chamaemorus*, *Salix*, *Vaccinium*, *Vaccinium* type, *Vaccinium uliginosum* type, *Veratrum* type
Switch plants	*Ephedra*, *Ephedra alata* type, *Ephedra distachya*, *Ephedra distachya* type, *Ephedra fragilis*, *Ephedra fragilis* type, *Ephedra fragilis* var *campylopoda*, *Ephedra major* type
Climber/liana/vine	*Calystegia*, *Calystegia sepium*, *Clematis*, *Clematis* type, Convolvulaceae, *Convolvulus*, *Convovulus arvensis*, *Cuscuta*, *Glycine*, *Hedera*, *Hedera helix*, *Humulus*, *Humulus lupulus*, *Lonicera*, *Periploca*, Ranunculaceae, *Smilax*, Solanaceae, *Solanum*, *Solanum dulcamara*, *Tamus communis*, *Vitis*, *Vitis vinifera*
Boreal low-to-high shrub	*Cotoneaster*, *Erica*, *Erica* type, Ericaceae, Ericaceae type, *Myrica*, Pinaceae, *Pinus*, *Pinus* (Diploxylon), *Pinus* subg. *Pinus*, *Ribes*, *Ribes* cf. *montigenum*, *Vaccinium*, *Vaccinium* type
Temperate low-to-high shrub	Amaranthaceae/Chenopodiaceae, *Atropa*, Berberidaceae, *Berberis*, *Calluna*, *Calluna vulgaris* type, Chenopodiaceae, *Cistaceae*, *Cistus*, Convolvulaceae, *Cornus*, *Cornus mas*, *Cornus mas/Cornus suecica*, *Cornus sanguinea*, *Cotoneaster*, *Crataegus*, *Crataegus* type, *Daphne*, *Erica*, *Erica* type, Ericaceae, Ericaceae type, *Hippophae*, *Hippophae rhamnoides*, *Lycium*, *Prunus*, *Prunus spinosa* type, *Prunus* type, Rhamnaceae, *Rhamnus*, *Rhododendron*, *Rhododendron ponticum*, *Ribes*, *Rosa*, *Rosa* type, *Rubus fruticosus*, Rutaceae, *Sambucus*, *Sambucus ebulus*, *Sambucus nigra* type, *Sambucus* type, Scrophulariaceae, Thymelaeaceae, *Thymus*, *Viburnum*, *Viburnum* type
Warm-temperate low-to-high shrub/small tree	*Abutilon*, Amaranthaceae/Chenopodiaceae, *Arceuthobium*, Berberidaceae, *Caragana*, *Carpinus*, *Carpinus orientalis*, *Carpinus orientalis* type, *Carpinus orientalis/Ostrya*, *Celastrus*, *Cercis siliquastrum*, Chenopodiaceae, *Cistaceae*, *Cistus*, *Cistus incanus*, *Cistus salviifolius*, *Colutea*, Convolvulaceae, *Convolvulus*, *Cornus*, *Cornus mas*, *Cornus mas/Cornus suecica*, *Cotinus*, *Daphne*, *Elaeagnus*, *Erica*, *Erica* type, Ericaceae, Ericaceae type, *Euonymus*, *Fontanesia philliraeoides*, *Frangula*, *Frangula alnus*, *Fraxinus ornus*, *Genista* type, *Jasminum*, *Jasminum fruticans*, *Juniperus*, *Juniperus communis*, *Juniperus* type, *Lagonychium* type, *Lavatera* type, Leguminosae, *Ligustrum*, *Morus*, Myrtaceae, *Myrtus*, Oleaceae, *Paeonia*, *Paliurus*, *Paliurus spina-christi/Rhamnus*, *Paliurus/Rhamnus*, *Phillyrea*, *Phillyrea angustifolia*, *Pistacia*, *Prosopis*, Rhamnaceae, *Rhamnus*, *Rhamnus* subg. *Frangula*, *Rhododendron*, *Rhus*, *Rhus coriaria*, *Ruta*, *Rutaceae*, *Sambucus*, *Sambucus* type, Solanaceae, *Solanum*, *Syringa*, Thymelaeaceae, *Thymus*, *Ulex* type, *Vitex agnus-castus*
Xerophytic shrub	*Alhagi*, Amaranthaceae/Chenopodiaceae, *Artemisia*, *Artemisia* type, *Atraphaxis*, Capparidaceae, *Capparis*, Chenopodiaceae, *Chrozophora*, Cistaceae, *Cistus*, *Cistus ladanifer*, *Cistus salviifolius*, *Cotinus*, *Erica*, *Erica* type, Ericaceae, Ericaceae type, *Euphorbia*, *Juniperus*, *Juniperus* type, *Lycium*, *Myricaria*, *Nitraria*, *Ononis* type, *Paliurus*, *Paliurus spina-christi/Rhamnus*, *Paliurus/Rhamnus*, Rhamnaceae, *Rhamnus*, *Ruta*, Rutaceae, *Sarcopoterium*, Thymelaeaceae, *Thymus*, *Trachomitum*, *Zygophyllum*
Boreal cold-deciduous malacophyll broadleaved tree	*Alnus incana*, *Alnus viridis*, *Betula*, *Populus*, *Salix*
Boreal evergreen needle-leaved tree	*Abies*, *Picea*, *Picea abies*, Pinaceae, *Pinus*, *Pinus* (Haploxylon), *Pinus cembra*, *Pinus peuce*
Boreal needle-leaved deciduous tree	*Larix*, Pinaceae
Cool-temperate evergreen needle-leaved tree	*Picea*, *Picea orientalis*, Pinaceae
Eurythermic evergreen needle-leaved tree	Cupressaceae, *Cupressus*, *Juniperus*, *Juniperus communis*, *Juniperus* type, Pinaceae, *Pinus*, *Pinus* (Diploxylon), *Pinus* subg. *Pinus*

(Continues)

TABLE 2 (Continued)

Plant functional type	Constituent taxa
Temperate (frost-induced late budburst) cold-deciduous malacophyll broadleaved tree	*Acer*, *Acer platanoides*, Aceraceae, *Cornus*, *Cornus mas*, *Cornus mas/Cornus suecica*, *Corylus*, *Corylus avellana*, *Fraxinus*, *Fraxinus angustifolia*, *Fraxinus excelsior*, *Fraxinus excelsior* type, *Malus*, *Malus sylvestris* type, *Malus* type, *Populus*, *Prunus*, *Prunus spinosa* type, *Prunus* type, *Pyrus*, *Quercus*, *Quercus* (deciduous), *Quercus robur* type, *Salix*, *Sorbus*, *Sorbus* type, *Tilia*
Temperate (spring frost tolerant) cold-deciduous malacophyll broadleaved tree	*Acer campestre* type, *Aesculus*, *Carpinus*, *Carpinus betulus*, *Cercis siliquastrum*, *Fagus*, *Fagus sylvatica*, *Frangula*, *Frangula alnus*, *Fraxinus ornus*, Leguminosae, *Morus*, *Pistacia*, *Prunus* type, *Quercus*, *Quercus cerris*, *Quercus cerris* type, *Quercus frainetto*, *Quercus ithaburensis*, *Rhamnus* subg. *Frangula*, *Syringa*, *Ulmus*, *Ulmus glabra*, *Ulmus laevis*, *Ulmus/Zelkova*
Temperate (spring frost intolerant) cold-deciduous malacophyll broadleaved tree	*Carpinus*, *Carpinus orientalis* type, *Carpinus orientalis/Ostrya*, *Carya*, *Castanea*, *Castanea sativa*, *Celtis*, *Celtis reticulate*, *Ceratonia*, *Fagus*, *Fagus orientalis*, Juglandaceae, *Juglans*, *Juglans regia*, Leguminosae, *Liquidambar*, *Ostrya*, *Ostrya* type, *Parrotia persica*, *Platanus*, *Pterocarya*, *Pterocarya fraxinifolia*, *Punica*, Rhamnaceae, *Rhamnus*, *Styrax*, *Ulmus/Zelkova*, *Zelkova*
Temperate evergreen needle-leaved tree	*Abies*, *Abies nordmanniana*, *Cedrus*, Pinaceae, *Pinus*, *Pinus* (Diploxylon), *Pinus* (Haploxylon), *Pinus* subg. *Pinus*, *Pinus sylvestris*, *Taxus*
Warm-temperate evergreen malacophyll broadleaved tree	*Acacia*, *Acacia greggii*, *Acalypha*, *Citrus*, *Diospyros*, *Ficus carica*, *Ilex*, Leguminosae
Warm-temperate sclerophyll tree	*Acalypha*, *Arbutus*, *Buxus*, Leguminosae, *Nerium*, *Olea*, Oleaceae, *Quercus*, *Quercus* (evergreen), *Quercus calliprinos*, *Quercus coccifera*, *Quercus coccifera* type, *Quercus ilex*, *Quercus ilex* type, Rutaceae
Warm-temperate needle-leaved evergreen tree	Cupressaceae, *Cupressus*, *Juniperus*, *Juniperus sabina*, *Juniperus scopulorum*, *Juniperus* type, Pinaceae, *Pinus*, *Pinus* (Diploxylon), *Pinus* (Haploxylon), *Pinus pinaster*
Tuft tree	*Phoenix*

basins sample a pollen source area more representative of the heterogeneous and fine-scaled patterning of vegetation in a region characterized by both topographic and climatic diversity (Bunting, Gaillard, Sugita, Middleton, & Broström, 2004; Prentice, 1985; Sugita, 1994).

Although the number of correct assignments overall is limited, many samples are assigned to closely related biomes (Tables 3 and 4). The method is most successful at predicting the distribution of cool mixed evergreen needleleaf and deciduous broadleaf forest (69%), temperate deciduous malacophyll broadleaf forest (57%) and evergreen needleleaf woodland (54%). Desert (25%) and graminoids with forbs (23%) are the most accurately predicted of the open vegetation types; shrublands are poorly predicted (Table 3). There is a bias towards reconstructing landscapes that are more wooded than observed: desert, grassland and shrubland biomes are more likely to be reconstructed as woodland or forest types (Table 3). The bias towards reconstructing more wooded landscapes is a known feature of biomization (e.g. Bigelow et al., 2003; Prentice & Jolly, 2000) and occurs because many herbaceous taxa (e.g. Amaranthaceae, some *Artemisia*) are under-represented in pollen assemblages while many tree species are well dispersed and therefore dominate the regional vegetation signal (Prentice, 1988; Sugita, 2007).

The misclassification of forest types is more complex, in that samples tend to be allocated both to woodland and to other forest types (Table 3). The biomization procedure does not yield reconstructions of warm-temperate deciduous malacophyll broadleaf forest, and samples from this ecosystem are generally classified as temperate deciduous malacophyll broadleaf forest. There is a tendency to predict mixed forest types at the expense of either deciduous or evergreen forests. Thus, although the prediction of temperate deciduous malacophyll broadleaf forest is reasonable (57%), 17% of the sites are incorrectly attributed to mixed forest types. It is not surprising that mixed forest types should be over-predicted compared to observations, given that characteristic taxa such as *Pinus* are well dispersed and therefore likely to be present as contaminants in samples from other types of forest.

The misclassification of samples in the biomization procedure does not reflect the impact of human activities on the vegetation. The removal of sites that are in areas classified as anthropogenically modified by GLC2000 (Table 6) reduces the number of sites available for comparison from 1,181 to 750 but does not improve the proportion of correct predictions (33%). This finding is consistent with results from other regional biomizations (e.g. Prentice et al., 1996; Williams, Webb, Richard, & Newby, 2000), which showed that correct prediction is possible even in heavily impacted environments providing remnants of natural vegetation were present in the landscape. Despite the fact that anthropogenic modification of the landscape might be expected to have changed within the 250 years used as the window to select the modern samples, comparisons based on shorter (50, 100 year) time intervals neither improve nor degrade the quality of the match between reconstructions and observations.

4 | DISCUSSION

The biomization procedure provides reasonable reconstructions of the geographic and elevation patterns of modern vegetation in the Eastern Mediterranean–Black Sea–Caspian-Corridor (Figure 4). Our

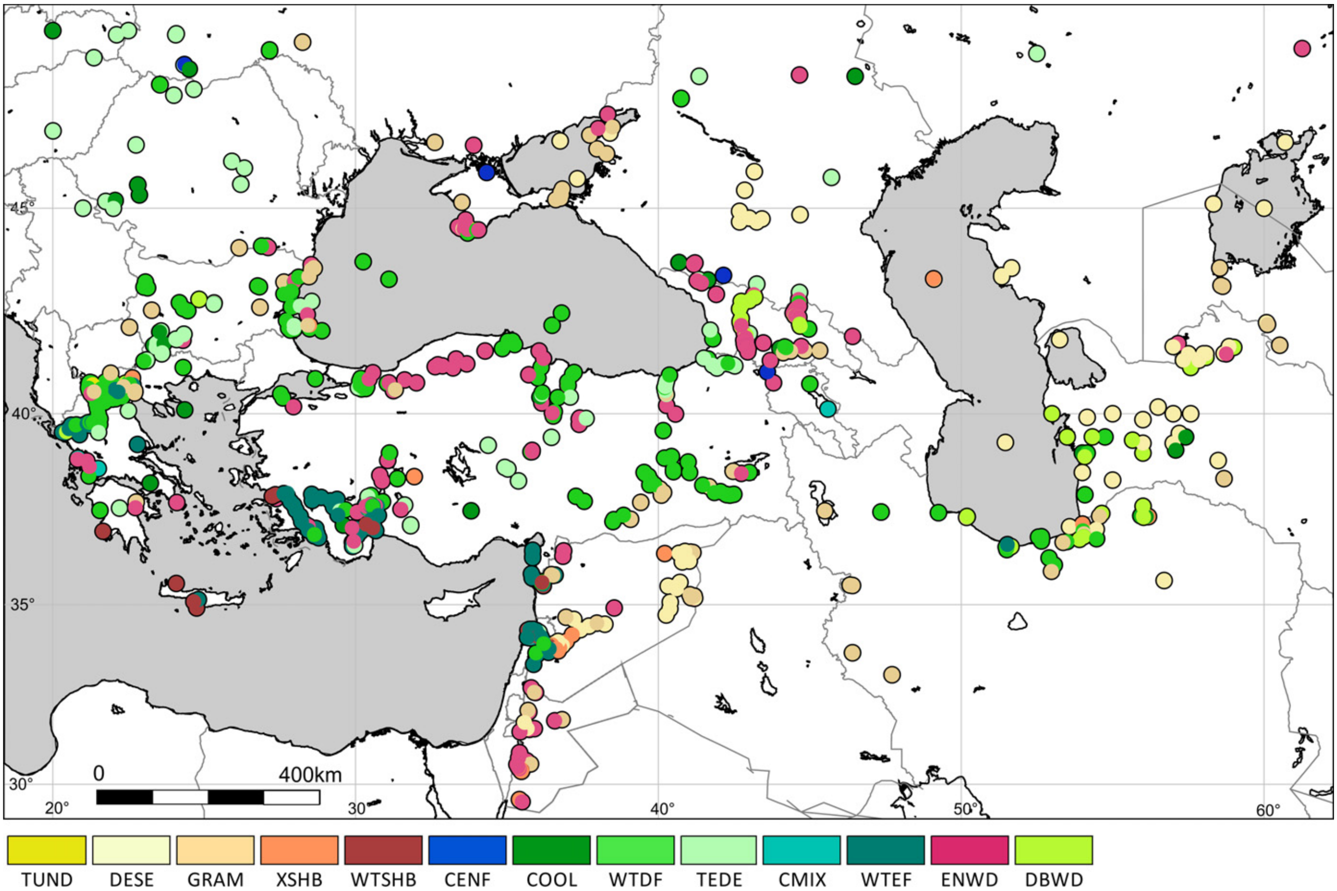

FIGURE 3 Map showing reconstructed modern biomes. The biome codes are TUND: tundra, DESE: desert, GRAM: graminoids with forbs, XSHB: xeric shrubland, WTSHB: warm-temperate evergreen sclerophyll broadleaf shrubland, CENF: cold evergreen needleleaf forest, COOL: cool evergreen needleleaf forest, WTDF: warm-temperate deciduous malacophyll broadleaf forest, TEDE: temperate deciduous malacophyll broadleaf forest, CMIX: cool mixed evergreen needleleaf and deciduous broadleaf forest, WTEF: warm-temperate evergreen needleleaf and sclerophyll broadleaf forest, ENWD: evergreen needleleaf woodland, and DBWD: deciduous broadleaf woodland

analysis suggests that the technique is capable of discriminating deserts from shrublands, the prevalence of woodlands in moister lowland sites, and the presence of temperate and mixed forests at higher elevations and in coastal sites around the Mediterranean Sea, Black Sea and Caspian Sea. The quantitative comparison with the EVM and FGAM maps is poor, with only 44% correct assignments in Europe and 33% overall. This is not improved by excluding sites that lie in regions that are classified as anthropogenically altered by the GLC2000, or by selecting pre-20th century samples. The degree of correspondence between EVM and FGAM, in the area where they overlap, is only 33%, and this suggests that the apparently poor quantitative performance of the biomization procedure may be partly due to problems with the target maps themselves. The EVM and FGAM classifications emphasize floristic composition rather than vegetation structure–the boundaries between, for example, woodlands and forests, and between broadleaved and mixed forest are not well defined in these maps. The difficulty of obtaining reliable maps of potential vegetation has been a problem for previous regional biomizations. Our field knowledge of the vegetation of this region suggests that the biome reconstructions are reasonable. However, it would be desirable to be able to make more robust quantitative analyses against structurally defined vegetation classifications based on systematic field descriptions.

The biases identified in the quantitative comparisons are consistent with known problems in interpreting regional vegetation from pollen. Thus, there is an over-representation of woody taxa resulting in the classification of open vegetation types (desert, grassland, shrubland) as woodlands and/or forest. Herbaceous taxa are frequently poorly represented in pollen assemblages, while many tree species are over-represented (Prentice, 1988; Sugita, 2007). Similarly, many shrubs from the more arid regions of the study area have low pollen production (e.g. *Ziziphus*) and are rarely found in pollen samples, leading to difficulties in discriminating shrubland from either more open vegetation or woodlands. Pollen production biases were regarded as a problem in the biomization of the former Soviet Union (Tarasov et al., 1998) and more generally in the northern mid- to high-latitudes (Bigelow et al., 2003). Attempts to take pollen productivity into account in regional biomizations to date have been relatively crude (e.g. upweighting or downweighting specific taxa, such as *Larix*: Bigelow et al., 2003). However, there are a number of new techniques that have been developed to correct for biases in pollen productivity, including the application of correction factors based on

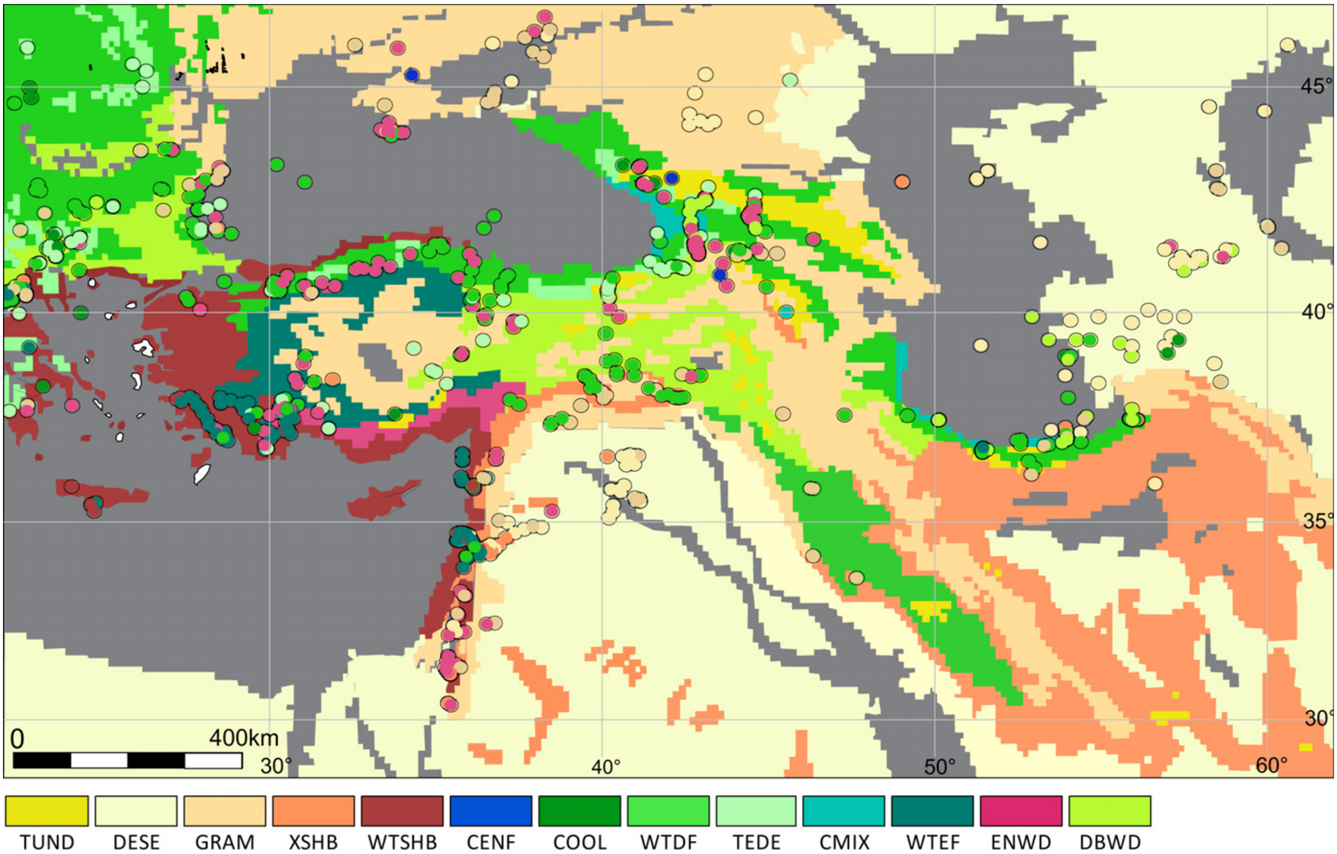

FIGURE 4 Map showing reconstructed modern biomes superposed on map of observed biomes. The biome codes are TUND: tundra, DESE: desert, GRAM: graminoids with forbs, XSHB: xeric shrubland, WTSHB: warm-temperate evergreen sclerophyll broadleaf shrubland, CENF: cold evergreen needleleaf forest, COOL: cool evergreen needleleaf forest, WTDF: warm-temperate deciduous malacophyll broadleaf forest, TEDE: temperate deciduous malacophyll broadleaf forest, CMIX: cool mixed evergreen needleleaf and deciduous broadleaf forest, WTEF: warm-temperate evergreen needleleaf and sclerophyll broadleaf forest, ENWD: evergreen needleleaf woodland, and DBWD: deciduous broadleaf woodland. The mapping scale for the observed biomes is relatively coarse and thus obscures vegetation changes with topography that are discriminated in the reconstructions

modern relationships between tree and pollen abundance (Williams, 2002) and the landscape reconstruction algorithm (LRA: Sugita, 1994, 2007; Sugita, Hicks, & Sormunen, 2010). It may be possible to improve the reconstruction of open vegetation in biomization using such techniques to convert pollen assemblages into estimates of taxon abundance on the landscape. However, both techniques require more detailed information about taxon abundance, pollen productivity and pollen dispersal rates than is currently available for the EMBSeCBIO region.

The over-representation of woody taxa is also an issue for the reconstruction of open vegetation types characteristic of high elevation sites. Pollen transport from lowlands has been shown to have an important impact on the pollen rain at sites above timberline in several mountainous regions within the study area (Bozilova & Tonkov, 2000; Connor et al., 2004; Tonkov, Hicks, Bozilova, & Atanassova, 2001). Biases resulting from upward transport of pollen in mountain regions have been noted in previous regional biomization studies (e.g. Takahara et al., 2000; Tarasov et al., 2000). Again, the application of modern analogue or LRA techniques to compensate for differential pollen transport would be useful here.

The fact that some pollen taxa are assigned to multiple PFTs may exacerbate the uncertainty in reconstructing biomes. The use of macrofossils has been suggested as an alternative way of refining assignments for ambiguous taxa (Birks & Birks, 2000; Cordova et al., 2009) because macrofossils are generally identifiable at species level. Macrofossil data are available for only eight of the sites in our modern data set. Using the species-level information from the macrofossils to change taxon-PFT assignments did not change the biome allocation for any of these sites. This limited evaluation suggests that the use of macrofossil information will not improve reconstructions through biomization. Nevertheless, systematic analysis of macrofossil assemblages would allow a more rigorous test of this conclusion, and the collection of macrofossil data at new pollen sites would be useful.

Human disturbance is often invoked as an explanation for poor representation of modern vegetation patterns from modern pollen surface samples, particularly in regions with a long history of cultivation. However, our analyses do not suggest that there are more mismatches between observed and reconstructed biomes in areas classified as urban or cultivated. Thus, the biomization procedure

TABLE 3 Comparison of biomes as predicted by the Eastern Mediterranean–Black Sea–Caspian-Corridor biomization procedure and observed biomes. The observed biomes are derived from The European Vegetation Map (EVM, Bohn et al., 2003) for the European sector and The *Physico-Geographic Atlas of the World* (FGAM, Gerassimov, 1964) for the remainder of the region. The order of the biomes reflects the order used in the tie-break procedure

	OBSERVED													
		TUND	DESE	GRAM	XSHB	WTSHB	CENF	COOL	WTDF	TEDE	CMIX	WTEF	ENWD	DBWD
PREDICTED	TUND	0	0	2	0	0	0	0	0	4	0	0	0	0
	DESE	0	38	11	2	1	0	0	3	0	0	0	1	0
	GRAM	0	19	44	10	4	0	4	1	15	0	7	3	9
	XSHB	0	10	11	3	4	0	0	0	1	0	0	4	0
	WTSHB	0	0	0	5	9	0	0	0	0	0	5	2	0
	CENF	0	0	3	1	0	1	1	0	0	0	0	0	0
	COOL	0	10	9	0	4	1	11	0	3	13	4	3	0
	WTDF	0	0	1	0	3	0	0	0	0	0	0	0	0
	TEDE	0	7	45	19	39	0	0	9	103	15	12	6	28
	CMIX	0	9	26	0	5	1	8	1	19	66	7	9	10
	WTEF	0	4	4	13	41	0	0	0	12	0	44	12	0
	ENWD	1	50	29	4	17	0	20	1	13	2	27	57	31
	DBWD	0	6	10	0	1	0	5	5	10	0	2	8	8

TABLE 4 Comparison of biomes as predicted by the Eastern Mediterranean–Black Sea–Caspian-Corridor biomization procedure and observed biomes in the European sector, as derived from The European Vegetation Map (EVM, Bohn et al., 2003)

	OBSERVED													
		TUND	DESE	GRAM	XSHB	WTSHB	CENF	COOL	WTDF	TEDE	CMIX	WTEF	ENWD	DBWD
PREDICTED	TUND	0	0	2	0	0	0	0	0	4	0	0	0	0
	DESE	0	0	9	0	0	0	0	0	0	0	0	1	0
	GRAM	0	0	35	0	0	0	4	0	14	0	7	2	5
	XSHB	0	0	6	0	0	0	0	0	1	0	0	1	0
	WTSHB	0	0	0	0	1	0	0	0	0	0	5	0	0
	CENF	0	0	3	1	0	1	1	0	0	0	0	0	0
	COOL	0	1	3	0	1	1	10	0	3	13	1	1	0
	WTDF	0	0	1	0	0	0	0	0	0	0	0	0	0
	TEDE	0	0	10	0	0	0	0	0	86	10	8	3	7
	CMIX	0	1	26	0	0	1	7	0	18	59	2	5	4
	WTEF	0	0	0	0	0	0	0	0	12	0	20	0	0
	ENWD	1	0	24	0	0	0	19	1	11	2	15	38	23
	DBWD	0	0	5	0	0	0	5	1	9	0	2	8	8

appears to provide a reliable estimate of regional vegetation patterns, even in heavily agricultural areas. This finding is consistent with previous attempts to reconstruct regional vegetation patterns through biomization (e.g. Prentice et al., 1996; Williams et al., 2000), which have consistently shown that anthropogenic impact is minor except at sites which are suboptimal for sampling regional vegetation characteristics (such as very small basins or forest hollows).

The most reliable reconstructions are obtained from samples from relatively small basins (Table 5). Many of the modern samples in the EMBSeCBIO database are from very large basins, including the Black Sea itself, and these have large pollen source areas and do not adequately represent the vegetation around the site. The topographic and climatic complexity of this region provides a further explanation for why better reconstructions are obtained from small basins. This suggests that rigorous site selection with respect to basin and catchment size will be necessary in applying the biomization technique to reconstruct past vegetation changes.

A more rigorous approach to the selection of sites based on geomorphic context may also be beneficial, particularly the exclusion of sites that are located in settings dominated by azonal vegetation

TABLE 5 Comparison of biomes as predicted by the Eastern Mediterranean–Black Sea–Caspian-Corridor biomization procedure and observed biomes, as derived from The European Vegetation Map (EVM, Bohn et al., 2003) and The *Physico-Geographic Atlas of the World* (FGAM, Gerassimov, 1964) for the remainder of the region, for small (<1 km) basins

	OBSERVED													
		TUND	DESE	GRAM	XSHB	WTSHB	CENF	COOL	WTDF	TEDE	CMIX	WTEF	ENWD	DBWD
PREDICTED	TUND	0	0	1	0	0	0	0	0	0	0	0	0	0
	DESE	0	0	0	0	1	0	0	0	0	0	0	0	0
	GRAM	0	0	19	0	0	0	0	0	2	0	0	0	1
	XSHB	0	0	1	0	0	0	0	0	0	0	0	0	0
	WTSHB	0	0	0	0	0	0	0	0	0	0	0	0	0
	CENF	0	0	0	0	0	0	0	0	0	0	0	0	0
	COOL	0	0	3	0	0	0	0	0	1	1	0	0	0
	WTDF	0	0	0	0	0	0	0	0	0	0	0	0	0
	TEDE	0	0	7	0	1	0	0	0	1	0	0	0	0
	CMIX	0	0	4	0	0	0	0	0	0	27	0	1	0
	WTEF	0	0	0	0	0	0	0	0	0	0	0	0	0
	ENWD	0	0	1	0	0	0	1	0	1	0	2	4	5
	DBWD	0	0	0	0	0	0	0	0	1	0	1	1	0

TABLE 6 Comparison of biomes as predicted by the Eastern Mediterranean–Black Sea–Caspian-Corridor biomization procedure and observed biomes, as derived from The European Vegetation Map (EVM, Bohn et al., 2003) and The *Physico-Geographic Atlas of the World* (FGAM, Gerassimov, 1964) for the remainder of the region, after removal of sites classified by GLC2000 as anthropogenically modified (artificial surfaces and associated areas, cultivated and managed areas, irrigated agriculture, mosaics including croplands)

	OBSERVED													
		TUND	DESE	GRAM	XSHB	WTSHB	CENF	COOL	WTDF	TEDE	CMIX	WTEF	ENWD	DBWD
PREDICTED	TUND	0	0	0	0	0	0	0	0	1	0	0	0	0
	DESE	0	34	5	2	1	0	0	1	0	0	0	0	0
	GRAM	0	12	26	6	2	0	4	0	5	0	7	0	2
	XSHB	0	7	9	3	4	0	0	0	0	0	0	3	0
	WTSHB	0	0	0	3	6	0	0	0	0	0	4	2	0
	CENF	0	0	2	1	0	0	1	0	0	0	0	0	0
	COOL	0	9	9	0	2	1	9	0	2	8	2	1	0
	WTDF	0	0	1	0	3	0	0	0	0	0	0	0	0
	TEDE	0	6	12	9	19	0	0	9	39	14	3	4	20
	CMIX	0	6	4	0	5	1	8	1	10	57	5	7	7
	WTEF	0	2	3	8	29	0	0	0	9	0	33	5	0
	ENWD	1	35	16	2	16	0	18	1	6	1	21	40	19
	DBWD	0	6	10	0	0	0	5	3	7	0	2	4	2

types. The pollen assemblages from riparian settings in semi-arid areas, for example, are generally dominated by trees. This results in the reconstruction of woodland or forest vegetation at such sites. While this is not wrong, strictly speaking, it provides little information about the regional vegetation that is more likely to be open steppe or xerophytic shrubland. A similar situation applies to pollen samples from wind-exposed coastal regions, where the vegetation is structurally similar to desert vegetation and reconstructions yield estimates of open vegetation and desert although the regional vegetation is forest. Cores from coastal lagoons and basins on the shelves of adjacent marine waters represent the regional vegetation better under these circumstances (Cordova et al., 2009). The exclusion of such atypical sites, combined with the exclusion of records from large basins, would yield a better reconstruction of regional vegetation patterns. However, semi-arid regions are frequently characterized by a mosaic of vegetation types reflecting local variability in environmental conditions, and thus, it may be desirable to preserve information from atypical sites to capture this variability.

The reconstructions of modern vegetation patterns in the EMBSeCBIO region are qualitatively reasonable. However, our analyses indicate that certain types of site (small basins, surface samples) give more reliable results than others. The interpretation of results from sites from geomorphic situations such as coastal lagoons or fluvial settings should be interpreted a reflecting local rather than regional vegetation. The over-representation of tree pollen in open vegetation is more difficult to deal with. The application of the LRA technique (Sugita, 1994, 2007; Sugita et al., 2010) would provide an obvious way to improve past vegetation reconstructions but requires a systematic effort to collect information about pollen productivity of key species in this region as well as detailed field studies of the relationship between pollen surface samples and vegetation at a sub-basin scale or to test alternative approaches (Mrotzek, Couwenberg, Theuerkauf, & Joosten, 2017). These studies are unlikely to be achieved rapidly. In the interim, it is possible to exploit the robust features of biomization. For example, although quantitative comparisons indicate that the reconstruction of open vegetation is poor (with only 33% of the observations being correctly predicted), these analyses show that when open vegetation is predicted it is correctly predicted in 64% of cases (Table 3). Thus, these reconstructions can be interpreted as a robust but minimal estimation of the extent of open vegetation and changes in the amount of open vegetation through time as a reflection of the response to changing climate.

The interpretation of reconstructions of past vegetation patterns in regions of complex topography and vegetation should always be interpreted with caution. However, our analyses suggest that biomization offers a reasonable approach to reconstructing vegetation patterns across the Eastern Mediterranean–Black Sea–Caspian-Corridor. In addition to improving our understanding of the vegetation response to past climate changes (Harrison & Prentice, 2003; Prentice, Harrison, & Bartlein, 2011), this will allow us to address specific regional issues including the impact of climate change on the availability of natural resources in a critical region for human cultural development (Turney & Brown, 2007).

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DATA ACCESSIBILITY

The information contained in Appendix S1 and S2 including the observed and reconstructed biome for each sample is available from https://doi.org/10.17864/1947.109 (Harrison, S.P. and Marinova, E., 2017. EMBSeCBIO modern pollen biomization. University of Reading Data set). The pollen counts from the surface samples have been submitted to EPD.

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BIOSKETCH

EMBSeCBIO (Eastern Mediterranean–Black Sea–Caspian BIOmes) is an international consortium aiming to reconstruct vegetation patterns and fire regimes in the Eastern Mediterranean–Black Sea–Caspian-Corridor over the past 30,000 years. These reconstructions will provide a better understanding of the environmental response to climate changes and of the interactions between climate, natural resources and humans in a climatically sensitive area at the crossroads of cultural exchanges between Asia and Europe in both modern and prehistoric times. EMBSeCBIO arose out of the BIOME6000 project and was a contribution to the work of the Palynology Group (Working Group 2) of the UNESCO-sponsored IGCP-521 program. EMBSeCBIO is currently led by Elena Marinova and Sandy P. Harrison.

Author contributions: EM and SPH are responsible for the database; EM, SPH, FB, VL and SC conducted the analyses; EM, SPH, SC, CC, SAGL and PM made the taxon classification; JA, EB, HC, CC, MD, Mf-M, NG, SJ, KK, UK, EK, ML, EN, ER, AR, LS, IT, ST, SAGL, PM and SC provided original pollen data; EM and SPH wrote the first draft of the manuscript, and all authors approved the final version.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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