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Modelling late Quaternary changes in plant distribution, vegetation and climate using pollen data from Georgia, Caucasus.

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Running title: Late Quaternary vegetation maps for Georgia

ABSTRACT

Aim: To use pollen data, numerical analysis and modelling to reconstruct late Quaternary vegetation and climate in a complex, mountainous environment.

Location: Georgia (Caucasus region)

Methods: Pollen data were assembled from various sources and used to map: (1) changing frequencies of individual taxa; (2) vegetation changes; and (3) reconstructed climatic parameters for the past 14,000 years. Numerical analyses were performed using two-way indicator species analysis (TWINSPAN), detrended correspondence analysis (DCA), the modern analogue technique (MAT) and weighted averaging (WA).

Results: Mapping of pollen taxa showed that Chenopodiaceae, *Artemisia* and *Ephedra* were most abundant in the study area during the late-glacial. *Betula* and *Corylus* expanded during the early Holocene, yielding to *Abies, Carpinus, Fagus, Quercus* and *Castanea*. *Picea, Pinus, Juglans* and *Ostrya*-type expanded during the late Holocene. Mixed forests grew in the moist, Black Sea refugium throughout the late Quaternary. Elsewhere in Georgia, the Pleistocene-Holocene transition is recorded as a shift from desert-steppes to oak-xerophyte communities and mixed forests. This kind of vegetation remained relatively stable until the mid-late Holocene, when coniferous forests and mountain grasslands advanced. DCA showed that rainfall was most strongly correlated with pollen composition in the study area ($r^2 = 0.55$). No temperature signal was detected. A weighted-averaging transfer function linking pollen percentages to annual precipitation was selected over a MAT model as it performed better when applied to a validation data set. Rainfall reconstructions indicate widespread aridity at the terminal Pleistocene, followed by a gradual increase in precipitation, peaking during the mid Holocene (7000-4000 cal. yr BP) and generally decreasing since then.

Main conclusions: On a regional scale, the results confirm previous studies of palaeovegetation and palaeoclimate in Western Asia. On a local scale, reconstructions from individual sites often diverge from the regional trend because of edaphic changes, ecological succession, human impacts and other disturbances. Some

of these factors are probably responsible for the increasing heterogeneity of Georgia's vegetation in the latter half of the Holocene.

Keywords: Caucasus, geographic information systems, Georgia, Holocene, modelling, refugia, palaeoclimate, palaeovegetation, palynology

INTRODUCTION

Pollen analysis has made a substantial contribution to our understanding of how the world's plant populations have changed through time. The distribution and abundance of pollen taxa reflect, on a regional scale, spatial variations in the composition of plant communities and biomes (Wright, 1967; Huntley & Birks, 1983; Haberle & Bennett, 2001). This, in turn, provides information on the prevailing macroclimate (Huntley *et al.*, 1995; Seppä *et al.*, 2004). Hence, if the network of well-dated pollen records in a particular area is large enough, the data can be analysed and mapped to show: (i) changing distributions and abundances of individual taxa; (ii) changing spatial patterns in reconstructed vegetation; and, (iii) broad-scale variations in the palaeoclimate.

These maps provide a rich source of information on how the present-day distribution of plant species, and the communities of which they are a part, came about. Palaeoclimatic reconstructions based on pollen can be usefully compared to other palaeoclimatic proxies (e.g. chironomids, tree rings, stable isotopes) to bring about a more refined understanding of past climatic change.

Reconstructing past vegetation and climate, however, is not a straightforward task. Vegetation can be quantitatively reconstructed from pollen data in a variety of ways: by matching fossil pollen to modern analogues in the vegetation (e.g. Overpeck *et al.*, 1985; Fletcher & Thomas, 2007), by linking pollen taxa to plant functional types and thence to biomes (Prentice *et al.*, 1996; Tarasov *et al.*, 2000), and by theoretical modelling (Sugita, 2007; Hall & McGlone, 2001).

Past climatic parameters (such as temperature, precipitation and others) have been reconstructed most commonly using the modern analogue technique (e.g. Cheddadi *et al.*, 1998; Solovieva *et al.*, 2005) and various forms of weighted averaging (e.g. Seppä & Birks, 2001; Prebble & Shulmeister, 2002). These are space-for-time substitution methods that calibrate the modern climate with modern pollen to produce a transfer function applicable to fossil samples (Jackson & Williams, 2004). They have recently come under scrutiny because the resultant transfer functions may be dominated by spatial autocorrelation, subject to over-fitting and based on dubious ecological assumptions (Jackson & Williams, 2004; Telford & Birks, 2005; Belyea, 2007).

Much of the uncertainty in reconstructing palaeoclimate from pollen data can be avoided by modelling only those climatic parameters that have a strong relationship with the pollen data (Seppä *et al.*, 2004). Assumptions such as climate-to-pollen equilibrium and representative sampling can be addressed using methods that favour parsimony over precision (cf. Telford & Birks, 2005). Such a method is applied here in an attempt to reconstruct the late Quaternary vegetational and climatic history of Georgia, in the mountainous Caucasus region.

The Caucasus is an attractive location for palaeoenvironmental studies in that it is a recognised 'hotspot' of biodiversity (Mittermeier *et al.*, 1999), has pronounced bioclimatic variation in relation to rainfall and altitude (Walter, 1974), has a long history of agriculture and pastoralism (Kiguradze & Sagona, 2003), and was an important refugium for thermophilous trees during glacial periods (Tumajanov, 1971).

Pollen analytical research has a considerable history in Georgia, which, in this regard, is the best investigated of all countries in the Caucasus. The first analyses were performed in the early 1930s. Even at that early stage, the difficulties of interpreting pollen diagrams in the Caucasus were recognised (Dokturovskii, 1936), leading authors to group pollen diagrams into geographic types (Neishtadt, 1957; Margalitadze, 1995). During the last 40 years, palynologists in Georgia have contributed significantly to Holocene studies, though much of their work is unknown outside the Caucasus.

Current opinion is divided on whether climatic changes were the dominant cause of vegetation change (e.g. Kvavadze & Rukhadze, 1989; Margalitadze, 1995), or whether human impacts and other disturbances exerted a greater influence (e.g. Gogichaishvili, 1990; Yazvenko, 1994; Connor *et al.*, 2007). A second debate concerns the Holocene vegetation history of Georgia: it is widely believed that almost all of Georgia was forested until recent centuries (e.g. Ketskhoveli, 1959; Nakhutsrishvili, 1999), while an alternative view holds that non-forest vegetation has a much longer history than this hypothesis would suggest (e.g. Avakov, 1982; Gogichaishvili, 1984). It is clear that these questions have considerable bearing on how the region's diverse plant communities came about and should be managed in future.

Continental-scale reconstructions (e.g. Tarasov *et al.*, 1998b, 2000) are too broad in their spatial and temporal scales to give a detailed impression of vegetation change in the study area, while other studies have focussed on a small geographic province (e.g. Kvavadze & Rukhadze, 1989) or ignored the region altogether (e.g. Khotinskiy, 1984). Despite the long history of palynological investigation in Georgia, a general overview of its late Quaternary vegetation and climate is notably lacking.

This paper aims to map changes in pollen abundances, vegetation and palaeoclimate in a complex, mountainous country.

STUDY AREA

Georgia is a nation of small size but great diversity, situated on the southern slope of the Caucasus Range (Figure 1). These mountains, rising over 5000 metres in elevation, form the northern limit of a country bordered to the west by the Black Sea coast, to the east by the semidesert lowlands of Azerbaijan, and to the south by the undulating volcanic plateaux of the Armenian Highlands.

Georgia's climate is strongly influenced by its rugged topography and the occurrence of moist, westerly airstreams originating over the Black Sea. Parts of

Western Georgia receive more than 2500 mm of rainfall annually. Mountain ranges create a rain-shadow over much of Eastern Georgia, where the driest parts receive less than 400 mm of rainfall each year and the climate is strongly continental. Average temperatures vary according to altitude and proximity to the Black Sea's maritime influence (AN GSSR, 1964; Tatashidze, 2000). A bioclimatic map is given in Figure 2.

Overlaid on its topographic and climatic variety, Georgia is home to considerable floristic diversity (Walter, 1974) and is located at the convergence of three major geobotanical territories: the Irano-Turanian, Euxinian and Euro-Siberian (Zohary, 1973). It is regarded as an important glacial refugium for thermophilous plants, hence the occurrence of species of *Zelkova, Juglans* and *Pterocarya* that largely vanished from Europe during the Pleistocene glacial periods (Tumajanov, 1971). Georgia's vegetation contains large numbers of endemics, at both a national and regional scale (Gagnidze *et al.*, 2002), and displays clear altitudinal zonation of vegetation belts in relation to temperature and precipitation gradients (Figure 2). This makes it a sensitive location for the study of past climatic change.

METHODS

Several methods were employed to satisfy the aims of this study, each discussed separately below:

Maps of changing pollen abundance

The first step in mapping pollen abundances at various times during the last 14,000 years was the compilation of a database. The database contained 236 fossil pollen spectra from 40 radiocarbon-dated cores, and 164 additional surface samples (Figure 1; Appendix S1, Supplementary Material). Only lake and mire sediment samples were used, avoiding moss- and soil-derived pollen spectra where issues of pollen taphonomy and source-area are often troublesome (Hicks, 2001). Data were drawn from published pollen diagrams and unpublished data generously provided by Jacqueline van Leeuwen, Erika Gobet and Brigitta Ammann (Institute of Plant Sciences, University of Bern). Some data were available as raw counts, but most were measured from diagrams by hand. We avoided data held in the Global Pollen Database because *Picea, Abies* and *Fagus* were absent from several records.

A calibrated (calendar) timescale was adopted with linear interpolation between dated levels. Occasionally, biostratigraphic markers such as the Pleistocene-Holocene boundary or the *Juglans* expansion were used to increase age control. Radiocarbon-dated pollen diagrams from the study area are the exception rather than the rule: 42 published pollen diagrams (apart from those used here) could not be used because they lack any independent age control. Sediments in the area are generally inorganic and there is limited access to accelerator mass spectrometer (AMS) dating.

As for sample selection, the sample nearest each 1000-year interval was read from the diagram. The sample was rejected if it appeared anomalous or degraded and the next closest sample was then used. Data were not smoothed between samples because of low temporal resolution in some diagrams. Pollen sums were calculated from the total tree and shrub pollen reported in each diagram. This was necessary because many of the area's pollen diagrams are calculated from separate arboreal and non-arboreal pollen sums. Trace proportions marked '+' were assigned a value of 0.5%. Non-arboreal pollen percentages were calculated individually from a sum including trees, shrubs, and the non-arboreal pollen type of interest (cf. Huntley & Birks, 1983). Taxa used in the analysis, including the plant species they represent, are listed in Appendix S2 (Supplementary Material).

Pollen frequencies for each 1000-year interval were mapped using geographic co-ordinates provided in published site descriptions. Maps were plotted using ArcGIS software (ESRI, 2005) on a base map kindly provided by Dr Lawrence Crissman (Crissman, 1995). Data are presented as graduated symbols rather than isopollen lines, because the latter can be misleading in rugged terrain with patchy site distribution.

Maps of reconstructed vegetation

This study adopts an approach similar to that used by Huntley (1988) to construct palaeovegetation maps of Europe. It uses two-way indicator species analysis (TWINSPAN: Hill, 1979) to classify the data into ecologically meaningful groups and mapping to trace the movements of these groups through time. This has an advantage over some other multivariate methods in that it does not assume that a particular fossil sample will have a modern analogue. It merely identifies the prevailing trend in the data and classifies pollen spectra according to similarities in composition. The thresholds and indicator species produced by the analysis have ecological and biogeographical meaning and can be used to classify other pollen spectra subsequently.

The dataset described above was reduced to include only sites where both arboreal and non-arboreal pollen were reported, accounting for the importance of Poaceae in grasslands and Chenopodiaceae in semideserts. An attempt to use arboreal pollen alone failed because of the prevalence of long-distance-transported *Pinus* and *Alnus* pollen in treeless environments. These taxa are useful indicators and could not be excluded from the pollen sum. *Cerealia*-type pollen, however, was excluded because few palynologists working in Georgia have counted or reported it. Pollen records from Sagarejo-Manavi and Bazaleti (Gogichaishvili, 1984) were also excluded because of probable fluvial pollen input at these sites. TWINSPAN pseudospecies cut-levels were set to 1, 2, 4, 10, 20, 30, 40, 60 and 80% to ensure that major taxa were selected as indicators and to reduce sensitivity to chance occurrences (Vermeersch *et al.*, 2003).

Maps of reconstructed climate

For the purposes of estimating past climatic parameters, it is important that these parameters are clearly reflected in pollen spectra today. Data on annual rainfall, average temperatures for January and July, and annual temperature ranges were obtained for each pollen site using data from the nearest meteorological station or from climatic maps (AN GSSR, 1964; Gulisashvili, 1964; Svanidze & Papinashvili, 1992; Tatashidze, 2000).

The pollen dataset was analysed using debugged detrended correspondence analysis (DCA: cf. Oksanen & Minchin, 1997) and correlations sought between climatic variables and ordination scores for modern pollen samples. Environmental data were included to determine their influence on the ordination, i.e. elevation, latitude, longitude and forest cover (10-km radius of site, measured from the most recent series of Soviet 1:100,000 topographic maps). Only climatic variables correlated to DCA scores were used for palaeoclimatic reconstruction.

A 'training set' of untransformed modern pollen data was modelled in the computer programme C2 (Juggins, 2006), using weighted averaging (WA) to derive climatic optima and tolerances for each pollen taxon. Other model types were also tried, including modern analogue technique (MAT), weighted averaging partial least squares (WAPLS) and non-parametric multiplicative regression (NMPR: McCune & Mefford, 2004). Model performance was assessed using correlation coefficients and bootstrap cross-validation. In addition, a dataset of 63 duplicates from sites with multiple samples was used to test the model. The best model was used for palaeoclimatic reconstruction. Palaeoclimatic anomalies were mapped in ArcGIS. Actual reconstructed values were superimposed onto the anomaly maps and, for diagrammatic purposes, interpolated by kriging based on an exponential semivariogram model.

The same transfer function was applied to AMS-dated pollen records from three sites to reconstruct changes of shorter duration. Sites selected were a high-rainfall coastal site in Western Georgia (Ispani), a subalpine site in the treeless plateaux of Southern Georgia (Aligol), and a site at the forest-steppe boundary in Eastern Georgia (Tsavkisi).

In addition to local trends, a generalised trend was produced by averaging reconstructed anomalies from all Georgian sites for each 1000-year increment. This was the most practical way to derive a regional palaeoclimatic curve, even though it relies on the assumption that every pollen record has equally good dating and that responses to climate change are uniform across a diverse region (see Chen *et al.*, 2008). The impact of records that violate this assumption should be diminished by the contribution of many more that do not.

RESULTS

Present-day patterns of pollen abundance

The present-day distribution of various pollen taxa reflects broad compositional differences in the vegetation (Figure 3). Euxine taxa, such as *Alnus*, are found in greatest proportions in Western Georgia, whereas more xeric taxa, including *Juniperus,* Chenopodiaceae and *Artemisia*, are more abundant in Eastern Georgia. *Abies* pollen is concentrated in northwestern Georgia and *Picea* is more important in the south. *Betula* and *Corylus* are abundant in the limestone country of the north. *Quercus, Juglans* and *Ulmus-Zelkova* are concentrated in the southeast, where forest borders on steppe. *Fagus* is widely distributed through middle altitude forests, and *Pinus* pollen, while also widespread, is most abundant in the treeless highlands.

Maps of changing pollen abundance

Temporal changes in the various pollen taxa show how the composition of Georgia's plant communities has altered over the past 14,000 years. Some taxa peaked at specific periods (e.g. *Picea*), while other taxa changed in their distribution over time (e.g. *Abies*). Changing pollen abundance has been mapped for *Abies, Alnus, Artemisia, Betula, Carpinus,* Chenopodiaceae*, Corylus, Fagus, Picea, Pinus,* Poaceae, *Quercus* and *Tilia* (Appendix S3, Supplementary Material).

Maps of reconstructed vegetation

A TWINSPAN dendrogram for the palaeovegetation reconstruction is shown in Figure 4. The major division of the dataset, explaining 23% of variance, separates samples high in *Alnus* from those with more Chenopodiaceae, Poaceae, *Quercus* and *Ostrya*-type (representing *Carpinus orientalis*). In geobotanical terms, this divides the moist Euxinian and Euro-Siberian provinces of the west and north of the country from the more arid Irano-Turanian province of the east and south.

From these, eight palaeovegetation units have been chosen for mapping:

1. Glacial desert-steppe unit (no modern analogue)
2. Semidesert-steppe unit
3. Oak-xerophyte unit (oak forest, open woodland, xerophyte scrub)
4. Mountain grassland unit (including pine parklands)
5. Mixed forest unit (beech, hornbeam, elm, fir and chestnut forests)
6. Alder swamp-forest unit

7. Subalpine unit (including dwarf woods and alpine herbfields)
8. Coniferous forest unit (forests or open woods of spruce and pine)

The present-day map of these units (Figure 5) clearly portrays the major vegetation patterns in the study area (cf. Figure 2). Alder swamps are located along the Black Sea coast, and above these a zone of mixed forest, with subalpine vegetation on the Caucasus Range and Anticaucasus (Lesser Caucasus) Mountains. The coniferous forests of Southern Georgia are accurately delineated, and eastward of these we pass over the treeless mountain grasslands of the South Georgian Uplands, through the narrow oak forest belt, along the xerophytic lower tree-line into the semidesert-steppe lowlands of Eastern Georgia (Figure 5).

Around 9% of reconstructions do not accord with their present-day vegetation (Table 1). In general, the misclassifications are explained by long-distance pollen transport, the site having a larger pollen source-area than the vegetation description provided, mixing of pollen from different altitudinal belts, or pollen sampling from basin edges rather than the centre. The misclassifications tend to push the reconstructed vegetation units upwards because of pollen transport to higher elevations, a problem characteristic of mountainous areas (Prentice *et al.*, 1996; Kvavadze, 1999b; van der Knaap *et al.*, 2001).

Reconstructed palaeovegetation maps are shown in Figure 6. From the few data of late-glacial age, it appears that mixed coniferous-deciduous forests grew in the Black Sea lowlands with subalpine vegetation at slightly higher elevations. *Abies* pollen was dominant in both cases. In Southern Georgia, arid desert-steppe extended westward into what is today a humid montane zone with beech and spruce forests.

The early Holocene saw desert-steppe vegetation yield to semidesert-steppe, oak-xerophyte and mixed forest vegetation. By 9000 calendar years before the present (cal. yr BP), regional differences in vegetation become apparent: mixed forests in Western Georgia, oak-xerophyte vegetation in Eastern Georgia, and subalpine vegetation in the mountains. This pattern barely changed from 8000 to 5000 cal. yr BP.

Coniferous forest appears on the maps at 5000 cal. yr BP, spreading eastward over the next few millennia. Mountain grasslands and alder swamps also expanded during this period. By 2000 cal. yr BP, oak-xerophyte vegetation had vanished from the map. Coniferous forest moved eastward into parts of Southern Georgia formerly home to mixed forests and subalpine meadows.

By 1000 cal. yr BP, mountain grasslands had expanded in Southern Georgia, with semidesert-steppes to the east and coniferous forests to the west. Alder swamps dominated the Colchis lowlands of Western Georgia, constricting mixed forests to foothills and mountain slopes. The last 1000 years saw coniferous forests return to parts of Southern Georgia and the re-establishment of oak-xerophyte vegetation near the Georgian capital, Tbilisi.

Maps of reconstructed climate

Three prevailing trends are identified from the detrended correspondence analysis (DCA). The first axis tends to separate samples from the eastern and western parts of the study area (Figure 7). In terms of pollen taxa (Table 2), this axis is positively correlated with *Alnus*, an indicator of high moisture levels (Ketskhoveli, 1959), and negatively correlated with taxa characteristic of dry environments (Connor *et al.*, 2004).

The second axis up-weights broadleaf taxa and down-weights coniferous taxa. Samples from deciduous forest zones have high scores on this axis compared to samples from coniferous zones. The third axis (not shown) gives high scores to samples from Southern Georgia and low scores to those from the north.

Comparing DCA results with environmental variables, it is clear that rainfall is a more important control on pollen composition in the study area than is temperature. Precipitation was positively correlated with DCA axis 1 ($r^2 = 0.55$); while temperature range (continentality) was negatively correlated with this axis ($r^2 = 0.29$). July and January temperature had positive correlations with DCA axis 2 ($r^2 = 0.10$ and 0.08 respectively) and negative correlations with DCA axis 3 ($r^2 = 0.10$). Because of the weak relationships between temperature parameters and the ordination results, we consider it unwise to attempt temperature reconstruction using the current dataset. The only other environmental variable to show any correlation was forest cover ($r^2 = 0.07$: axis 3).

Performance statistics for two rainfall reconstruction models are shown in Table 3. In terms of correlation coefficients, modern analogue technique produced reconstructions that were closer to the observed values than weighted averaging. Root mean squared errors of prediction (RMSEP) were similar for both techniques.

However, when the models were applied to the duplicate pollen dataset, both performed much worse than their performance statistics would suggest. Modern analogue technique performed particularly poorly.

Because we consider the duplicate dataset a more rigorous, realistic test of model performance than bootstrap cross-validation and also because spatial autocorrelation may be inherent in MAT models (Telford & Birks, 2005), we adopted the weighted averaging model for palaeoclimatic reconstruction.

Differences between observed and modelled rainfall were mapped (Figure 8) and show that weighted averaging tends to overestimate rainfall in Southern Georgia and underestimate it in the north. Since this pattern was consistently produced by all model types tested (i.e. WA, MAT, WAPLS, NPMR), it may be an artefact of the data rather than the method. Underestimates occur at alpine sites, where, presumably, a great deal of pollen is long-distance transported from lower (and drier) altitudes, diluting the local pollen signal (Fall, 1992). Overestimates occur along the Black Sea coast where *Alnus* pollen percentages are high because of poor soil drainage, rather than climatic factors. Overestimates in Southern Georgia are associated with high *Picea* percentages. The pattern reconstructed by extrapolating data points resembles the actual rainfall pattern (Figure 8), although inconsistencies occur in places where sites are lacking. High rainfall areas along the Black Sea coast and Main Caucasus Range are clearly delineated, as are the semi-arid areas of Southern and Eastern Georgia.

Rainfall reconstructions for the past 14,000 years are shown in Figure 9. The few available data indicate that very dry climates prevailed in southern and eastern Georgia during the late-glacial (<400 $mm.yr^{-1}$). In contrast, the climate of the Black Sea refugium may have been moister than it is today. Aridity waned during the early Holocene, establishing a rainfall pattern of more or less modern character after 9000 cal. yr BP. Rainfall increased at many sites during the mid Holocene (7000-4000 cal. yr BP). During the ensuing millennia the rainfall pattern in Western Georgia shifted, producing wetter conditions in the northwest and drier conditions in the southwest. Conditions 2000 cal. yr BP were generally wetter than present, becoming slightly drier around 1000 cal. yr BP.

A generalised rainfall trend for Georgia and three site-specific reconstructions are shown in Figure 10, alongside the Lake Van oxygen isotope curve (Lemke & Sturm, 1997), which could be considered the 'rain gauge' of the region. All four curves exhibit very different patterns, discussed at greater length below.

DISCUSSION

Late Quaternary vegetation

Our palaeovegetation maps are limited by the paucity of data and sites from the late-glacial, early Holocene and more arid parts of the study area. There may be large errors in dating where few absolute ages are available, not all vegetation types will be captured in the samples examined, and the successional transitions between some of them will be missed because of the 1000-year time interval chosen.

Nevertheless, they provide an overview of palaeovegetation development in the study area that will, no doubt, be improved by future empirical research.

According to our reconstruction (Figure 6), Georgia's vegetation has witnessed profound changes through the last 14,000 years. The history of each palaeovegetation unit helps illuminate the driving forces behind these changes. Glacial desert-steppe occurred in Eastern and Southern Georgia between 14,000 and 11,000 cal. yr BP. TWINSPAN indicators for this unit are Chenopodiaceae, *Artemisia* and *Ephedra*, which are all xerophytes prevalent in the most arid parts of the study area today (Connor *et al.*, 2004). Semidesert-steppe replaced glacial desert-steppe at the beginning of the Holocene, as rainfall increased.

Semidesert-steppe has the same palynological indicators, but with greater proportions of *Carpinus* and *Ostrya*-type, representing trees that are particularly common in low-altitude forests and scrub vegetation. Semidesert-steppe appeared at high elevations (1500-1900 m) during the early Holocene. Thereafter it is not represented on the palaeovegetation maps until the late Holocene. This can be attributed to a lack of pollen records from arid SE Georgia, rather than indicating its mid-Holocene absence.

The oak-xerophyte unit, indicated by *Quercus* and *Ulmus*, appeared at 10,000 cal. yr BP and populated areas of Eastern Georgia through the early-mid Holocene. From 4000 cal. yr BP onwards, oak-xerophyte vegetation was gradually replaced by mountain grasslands and semidesert-steppes. This is almost certainly related to human activities, as the fertile soils of oak- and elm-woods were first developed by early agro-pastoralists (Ketskhoveli, 1959; Dolukhanov, 1966). During the past millennium, oak-xerophyte vegetation has reclaimed some of its former area.

The mountain grassland unit has *Picea, Pinus* and *Ostrya*-type as indicators. These taxa have expanded at a rapidly accelerating rate during the last 4000 years. Mountain grasslands replaced areas of oak-xerophyte and subalpine vegetation, but were, at a few sites, invaded by coniferous forest during the late Holocene. Mountain grasslands today are often subjected to regular burning and grazing (Connor *et al.*, 2004), which may explain their late Holocene expansion.

Mixed forests derive from the glacial forest refugia of Western Georgia. Spreading eastward during the early Holocene, mixed forests enveloped large areas and changed in composition from *Abies*-dominated forest to varied associations of *Betula, Corylus, Carpinus, Fagus, Tilia, Ulmus* and *Castanea*. The moister conditions of the mid Holocene favoured mixed forests, particularly those dominated by *Fagus orientalis*. Beginning 5000 cal. yr BP, mixed forest distribution was curtailed by the expansion of swamp-forests on the Black Sea coast, coniferous forests to the south, and subalpine vegetation to the north.

Alder swamp-forests were present during the early Holocene, but proliferated during the mid-late Holocene. Sea levels in the Black Sea peaked around 4000 cal. yr BP, paludifying the low-lying areas of Colchis and restricting mixed forests to higher ground (Connor *et al.*, 2007). At some sites, mixed forests were able to reclaim areas of alder swamp-forest once sea levels stabilised.

Although conifers have always been constituents of Georgian forests, it is only during the mid-late Holocene that purely coniferous forests have expanded. It appears that *Picea orientalis* had its refugium in SW Georgia and moved eastwards into mixed forests and subalpine vegetation. Coniferous forests and mountain grasslands have a similar history and similar indicators. Hence it is tempting to ascribe coniferous forest expansion to human activity. At some sites coniferous forest indeed appears after disturbance events linked to human activity (Kvavadze & Efremov, 1996; Kvavadze & Rukhadze, 1989). At other sites (e.g. Didajaris Tba) the record shows a gradual change in forest composition, perhaps linked to climate change, soil weathering or ecological succession.

Finally, the subalpine unit begins its late-glacial history in piedmonts fronting the Black Sea (then a lake). By 10,000 cal. yr BP it appears at 1850 m elevation in Southern Georgia. Like the semidesert-steppe unit, the apparent Holocene expansion of subalpine vegetation stems from the few early Holocene pollen records from high altitudes. The sites available show that some areas of subalpine vegetation were invaded by mixed forest during the mid Holocene and by coniferous forest during the late Holocene.

Broadly speaking, our results are in harmony with palaeovegetation reconstructions produced by the ‘biomization’ method. Tarasov *et al.* (1998b, 2000) incorporated eleven Caucasian, mostly Georgian, sites in their reconstruction of northern Eurasia’s palaeovegetation at three stages: 18,000, 6000 and 0 ^{14}C yr BP. Their dataset differs from ours in the inclusion of cave sediments (i.e. Apiancha), alluvial sections (Manavi), and four sites without ^{14}C dating (Lisi, Lagodekhi, Kobuleti and Sukhumi).

The results show cool mixed forest and cool coniferous forest in Western Georgia at 18,000 ^{14}C yr BP, changing to temperate deciduous forest and cool coniferous forest by 6000 ^{14}C yr BP. For a single site in Eastern Georgia, the reconstruction indicates the persistence of steppe vegetation at all three stages.

Biome reconstructions better differentiate palaeovegetation types on climatic grounds – hence a transition from ‘cool’ to ‘warm’ deciduous forest between 18,000 and 6000 ^{14}C yr BP. Our analysis makes no such distinction, even though the composition of our ‘mixed forest unit’ changed at the Pleistocene–Holocene boundary. On the other hand, our results clearly separate the various open vegetation types (i.e. late-glacial desert-steppe, Holocene semidesert-steppe, mountain grassland and subalpine vegetation), an aspect that proved difficult using biomization (Tarasov *et al.*, 1998a).

Our study contributes a vast improvement in spatial coverage and temporal resolution for the Caucasus region. Using 1000-year time steps and many more sites, we are better able to show the dynamism of past vegetational responses to climate change, sea levels and human activity. This enables the results to be compared with similar reconstructions from neighbouring lands (e.g. Huntley & Birks, 1983; van Zeist & Bottema, 1991).

A notable feature of Georgia’s Holocene vegetation history is the development of an increasingly heterogenous landscape from around 3000 cal. yr BP onwards.

Andrič and Willis (2003) have observed a similar late Holocene phenomenon in Slovenia. They suggest that increasing heterogeneity was, in part, the product of burning and other prehistoric human activities. The same argument is applicable in the Georgian context, where, at several sites, major vegetation changes are obviously linked to human impact events (Gogichaishvili, 1990; Yazvenko, 1994; Connor & Sagona, 2005). By increasing landscape heterogeneity, the long interaction between humans and vegetation in the Caucasus may have contributed to maintaining biodiversity.

Palaeoclimatic reconstruction

Rainfall reconstructions (Figure 9) confirm the existence of widespread late-glacial aridity in the continental parts of Georgia, contrasting with moister climates in the Black Sea refugium. The Holocene brought a gradual increase in rainfall throughout the study area, peaking during the mid Holocene (7000-4000 cal. yr BP) and declining in the late Holocene, especially at the time of the 'Mediaeval climatic anomaly' (Bradley *et al.*, 2003).

This general trend is summarised by the 'master curve' in Figure 10. This represents the average rainfall anomaly for all sites at each 1000-year time step. It is an attempt to distil, from the varied regions of the Caucasus, an overarching signal of continental-scale climatic change that should rise above local factors (e.g. anthropogenic, taxonomic, topographic, edaphic). Such a curve is necessary to evaluate the palaeoclimatic relations between the Caucasus and other regions of

Western Asia, North Africa and Europe. Plainly, the curve presented here is less reliable for the period 14,000-11,000 cal. yr BP because there are so few late-glacial records and their dating is less certain.

Even so, this 'master curve' for Georgia is in agreement with isotopic and geochemical analyses from Lake Van, eastern Anatolia, and with palynologically derived treeline variations for Abkhazia, NW Georgia (Figure 10). Climatic events associated with the Younger Dryas and mid Holocene 'optimum' are clearly reflected in each of these regional trends.

The local rainfall trends in the lower part of Figure 10 are more difficult to interpret. The chronology of each record is reasonably secure, established through AMS radiocarbon dating and palynostratigraphy. Ispani-II is a coastal site on the Black Sea. Its rainfall trend is marked by a sudden and lasting decline around 3000 cal. yr BP. This decline is associated with increases in pollen of grasses, herbs and light-demanding shrubs likely to relate to prehistoric human activity (Connor *et al.*, 2007).

The second site, Aligol, is a small lake in the treeless highlands of Southern Georgia. The peak in its rainfall trend at 11,500 cal. yr BP contradicts a regional pattern of very dry climates. The Younger Dryas at Aligol, like other sites from the region, is characterised by high percentages of *Ephedra* and *Artemisia* pollen. Both of these xerophytes demand moisture during the growing season (Chikov, 1983; El-Moslimany, 1990), and it could be argued that summer evaporation was reduced under the colder or cloudier climate of the terminal Pleistocene, even though actual rainfall was very low (Roberts & Wright, 1993).

The third site, Tsavkisi, is situated in at the border of forest and steppe, near the Georgian capital, Tbilisi. Its rainfall trend exhibits the 3000 cal. yr BP decline and 2000 cal. yr BP increase seen in the regional trends, but little else. The vegetation dynamics of this small site are almost entirely dominated by the influence of grazing, indicated by abundant spores of *Sporormiella* dung fungi (Connor & Kvavadze, 2005). The rainfall trend is influenced by the site's land-use history, such that periods of heavy grazing mimic low rainfall and vice versa. At many sites, disturbance has promoted the expansion of chenopods, which also happen to be excellent palynological indicators of aridity. Such considerations demonstrate how local factors can impact upon palaeoclimatic reconstructions from small lakes and mires.

Previous studies of the region's Holocene palaeovegetation have tended to focus on temperature fluctuations as the driving force of vegetation change. Indeed, in the aforementioned study of Abkhazian treelines by Kvavadze *et al.* (1992), the timing and direction of the changes were interpreted largely in terms of temperature. It is therefore of some interest that we failed to detect a strong temperature signal in the Georgian pollen dataset used in this paper. This could be related to the limited number of taxa used, the method of percentage calculation, variable data quality, differences between regions, and other considerations such as spatial scale. It is also possible that interpretations of pollen taxa in the Caucasus have placed too much emphasis on their thermal indicator value.

Objective, pollen-based reconstructions indicate that the mid Holocene in Anatolia, Caucasus and southeastern Europe was characterised by summers that were relatively cool and wet (Tarasov *et al.*, 1999; Davis *et al.*, 2003). Low salinity and high water levels in Lake Van and the Aral Sea suggest increased moisture regionally, a pattern that extended well into Central Asia (Lemke & Sturm, 1997; Chen *et al.*, 2008). Likewise, data presented in this paper indicate that, in Georgia, the mid Holocene 'climatic optimum' was probably wetter rather than warmer. Thermophile taxa (e.g. *Quercus* and *Castanea*) that increased at some Georgian sites during the mid Holocene may have done so in response to Bronze Age human activities or seasonal shifts in rainfall rather than temperature increases.

In this regard, it is interesting to compare the oxygen isotope curve from Lake Mirabad in the Zagros Mountains, Iran (Figure 10). Stevens *et al.* (2006) interpret the curve as representing oscillations between a 'Mediterranean' rainfall regime dominated by winter precipitation and a more 'continental' climate of spring rains. If their interpretation is valid, then the periods of higher rainfall in the Caucasus occurred as the climate in the Zagros became more continental. Later arrival of rainfall in Georgia might favour *Quercus iberica* since these oaks tend to come into leaf slightly later than more mesic deciduous trees (e.g. *Carpinus betulus, Fagus orientalis*). Seasonal rainfall changes could also resolve the paradoxical occurrence of low lake levels in Southern Georgia during the wettest phase of the mid Holocene (Connor & Sagona, 2007). The mid-late Holocene expansion of coniferous forest in Georgia coincides with an increasingly Mediterranean rainfall regime in the Zagros region.

The precise nature of Western Asia's late Quaternary palaeoclimate and its interconnections with neighbouring climatic systems remain quite enigmatic, as evident in the literature (e.g. Roberts & Wright, 1993; Dalfes *et al.*, 1997; Wright *et al.*, 2003; Stevens *et al.*, 2006). Future research will no doubt show that climatic seasonality and variability in these environments is of far greater ecological and economic importance than gross measures of rainfall and temperature.

SUMMARY AND CONCLUSIONS

This study presents the first attempt to synthesise over 75 years of palynological data from Georgia, in the mountainous Caucasus region. The results are presented as a series of maps, which depict changing distributions of taxa and vegetation communities, as well as variations in the palaeoclimate, through the past 14,000 years.

The analyses indicate that the late-glacial in Georgia was a time of dry climates, with the widespread occurrence of desert-steppe vegetation and taxa such as Chenopodiaceae, *Artemisia* and *Ephedra*. Moist refugia existed in the Black Sea lowlands, where *Abies* was dominant in forests.

Conditions became wetter during the early Holocene, establishing mixed forests in the west and oak-xerophyte formations in the east. Initially, pioneers such as *Betula* and *Corylus* spread, followed by mesic forest taxa like *Abies, Carpinus betulus* and *Fagus* as the climate became less arid.

The mid Holocene seems to have been a time of relatively moist climates, with mixed forests and oak-xerophyte communities widespread. It was around this time that pine and spruce forests began to advance, a process that accelerated under the slightly drier climates of the late Holocene. Alongside these conifers, the expansions of *Juglans, Olea, Ostrya*-type and *Plantago* during the late Holocene bear the distinct marks of human impact.

At a regional scale, moisture changes have exerted a profound influence on the course of vegetation development in Georgia over the past 14,000 years. Late Quaternary rainfall variations in Georgia have followed the same general trend as in neighbouring areas of Western Asia, revealed through oxygen isotopic studies and pollen-based simulations.

At a local scale, human activities, edaphic changes, ecological succession, disturbance regimes and other factors have been crucial in the palaeoecology of individual sites, helping to explain present-day vegetation complexity, heterogeneity and biodiversity. Several modern plant communities appear to be relatively recent additions to the varied tapestry of Georgian landscapes.

An important outcome of this research is to show that reconstructed palaeoclimatic trends from individual sites can diverge from regional patterns of climate change. In mountain environments, local factors can produce highly individualistic pollen diagrams that tend to mask macroclimatic influences. While this may be overcome by selecting study sites where the pollen source-area is large, such sites are not always available or accessible. Satisfactory results can be obtained by combining palaeoclimatic anomalies from multiple small sites, so that site-specific influences are downplayed.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1. Caucasian pollen sites used in modelling and analysis, including details of location, dating control and sources. Numbering follows Figure 1.

Appendix S2. Pollen taxa used in the analysis, their weighted averaging statistics and plant species in Georgia they represent.

Appendix S3. Maps of changing pollen abundance for selected taxa in Georgia over the past 14,000 years (calibrated timescale).

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi (This link will take you to the article abstract).

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BIOSKETCHES

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Editor: John Birks.

FIGURE CAPTIONS

Figure 1. Map of Georgia showing the locations of study sites (for site details,

see Appendix S1, Supplementary Material). Inset: location of Georgia in Europe and Western Asia.

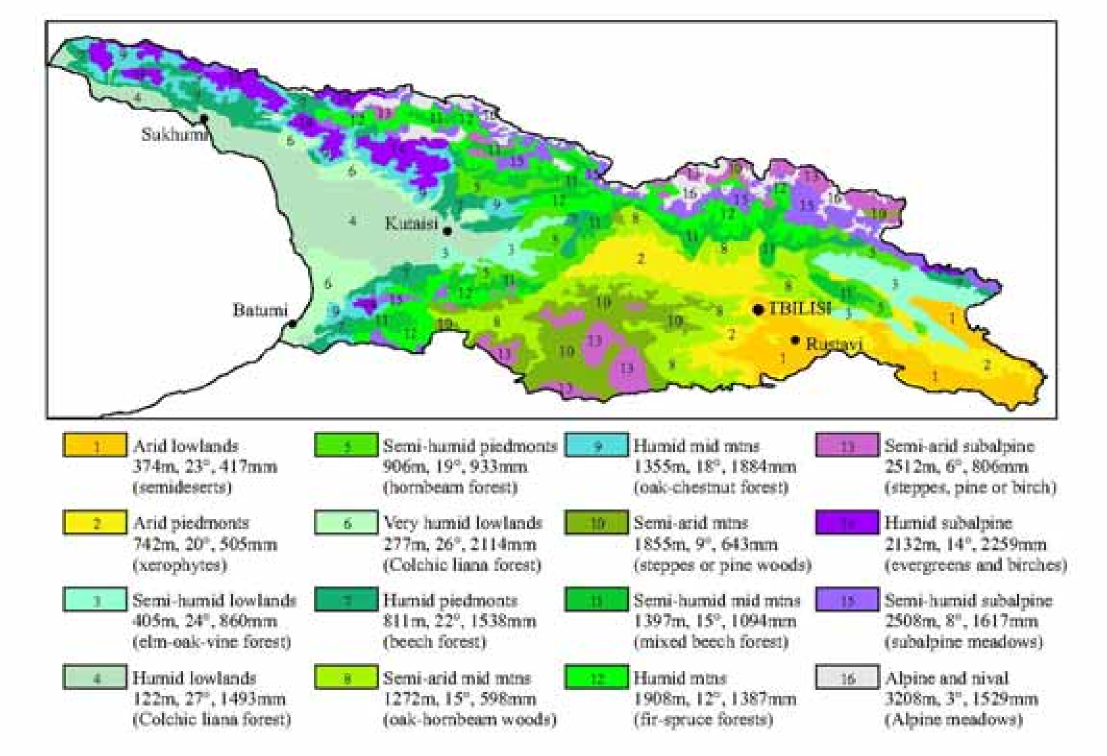
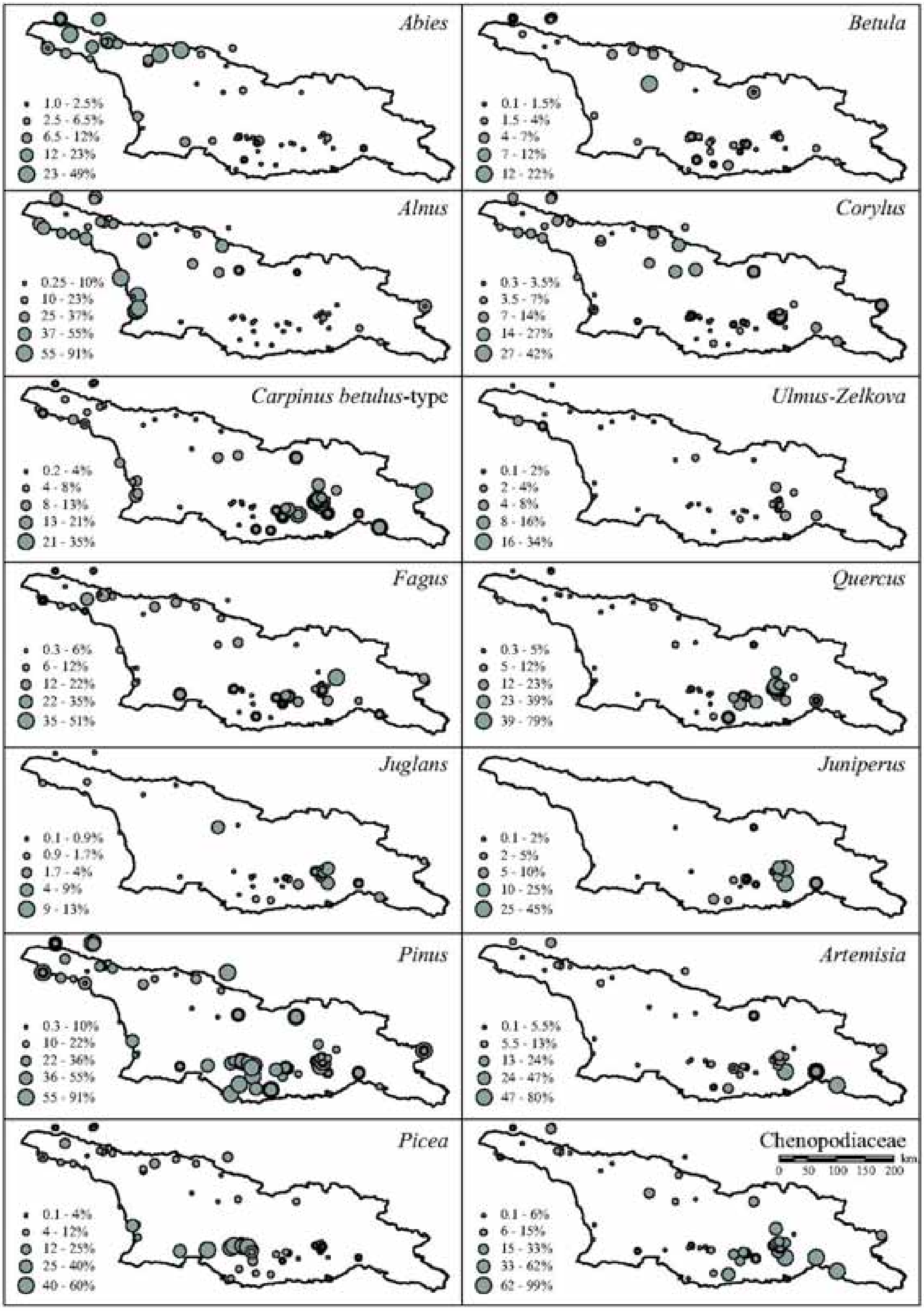


Figure 2. Bioclimatic map of Georgia. Average values for elevation (in m), July temperature (in ºC) and annual rainfall (in mm) are given for each zone. Major vegetation units associated with each zone are listed in parentheses. Map produced using the IsoCluster algorithm and maximum likelihood classification in ArcMap (ESRI, 2005) from a digital elevation model and maps of rainfall and temperature in the Georgian Atlas (AN GSSR, 1964).



Abies
1.0 - 2.5%
2.5 - 6.5%
6.5 - 12%
12 - 23%
23 - 49%
Betula
0.1 - 1.5%
1.5 - 4%
4 - 7%
7 - 12%
12 - 22%
Alnus
0.25 - 10%
10 - 23%
25 - 37%
37 - 55%
55 - 91%
Corylus
0.3 - 3.5%
3.5 - 7%
7 - 14%
14 - 27%
27 - 42%
Carpinus betulus-type
0.2 - 4%
4 - 8%
8 - 13%
13 - 21%
21 - 35%
Ulmus-Zelkova
0.1 - 2%
2 - 4%
4 - 8%
8 - 16%
16 - 34%
Fagus
0.3 - 6%
6 - 12%
12 - 22%
22 - 35%
35 - 51%
Quercus
0.3 - 5%
5 - 12%
12 - 23%
23 - 39%
39 - 79%
Juglans
0.1 - 0.9%
0.9 - 1.7%
1.7 - 4%
4 - 9%
9 - 13%
Juniperus
0.1 - 2%
2 - 5%
5 - 10%
10 - 25%
25 - 45%
Pinus
0.3 - 10%
10 - 22%
22 - 36%
36 - 55%
55 - 91%
Artemisia
0.1 - 5.5%
5.5 - 13%
13 - 24%
24 - 47%
47 - 80%
Picea
0.1 - 4%
4 - 12%
12 - 25%
25 - 40%
40 - 60%
Chenopodiaceae
km
0 50 100 150 200
0.1 - 6%
6 - 15%
15 - 33%
33 - 62%
62 - 99%

Figure 3. Present-day distribution of major pollen taxa in Georgia. Symbols are scaled differently for each map.

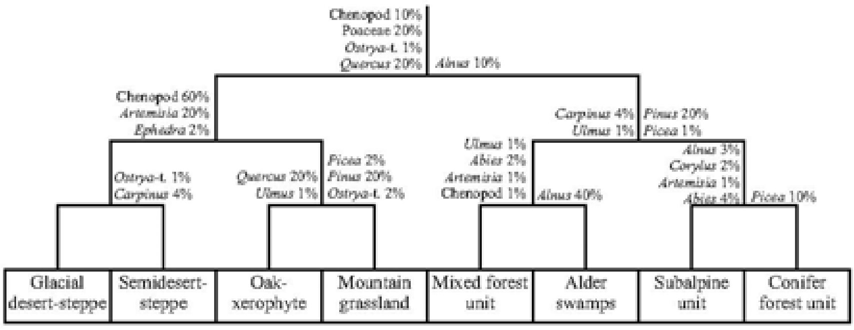


Figure 4. Two-way indicator species analysis (TWINSPAN) dendrogram. Taxa left of each split are negative indicators; taxa to the right are positive indicators. Indicator threshold values are given after taxa names.

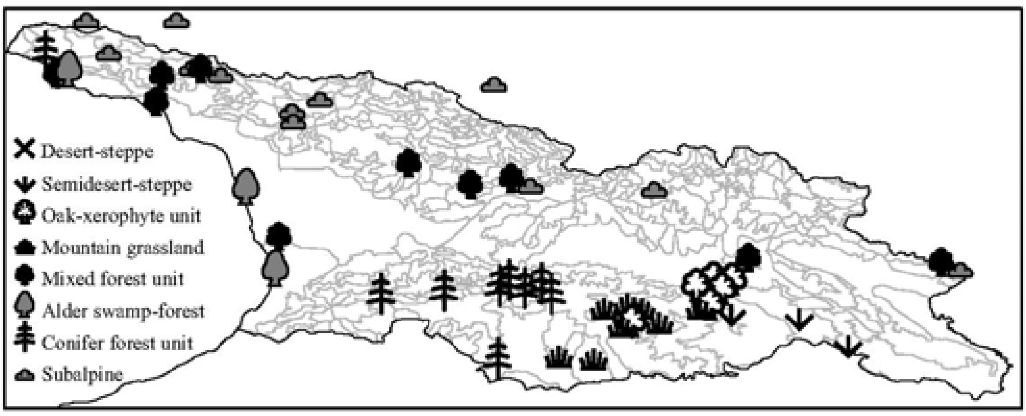
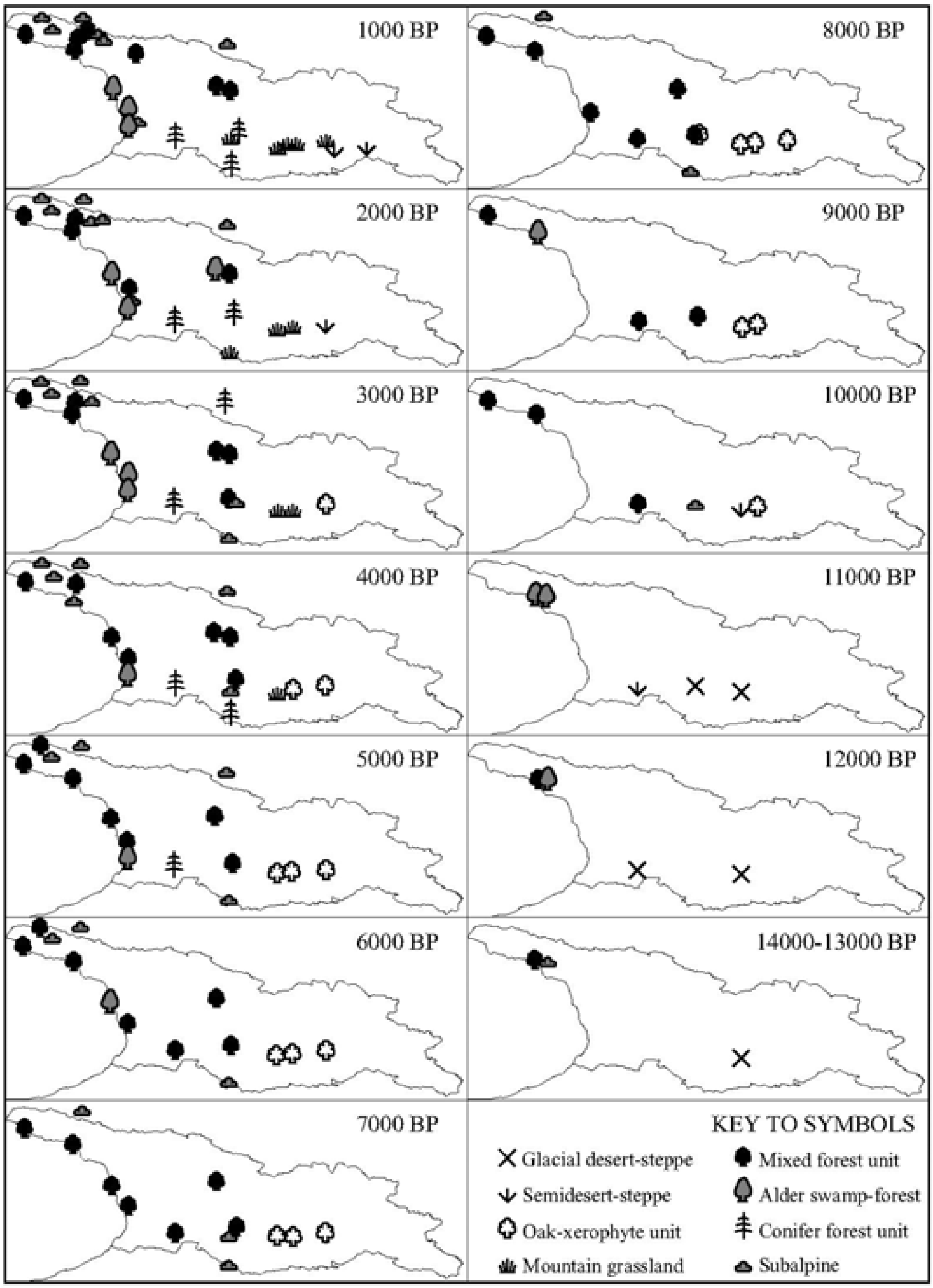


Figure 5. Map of present-day reconstructed vegetation at each pollen site in Georgia. Bioclimatic zones (Figure 2) are outlined in grey.



1000 BP
8000 BP
2000 BP
9000 BP
3000 BP
10000 BP
4000 BP
11000 BP
5000 BP
12000 BP
6000 BP
14000-13000 BP
7000 BP
KEY TO SYMBOLS
Glacial desert-steppe
Mixed forest unit
Semidesert-steppe
Alder swamp-forest
Oak-xerophyte unit
Conifer forest unit
Mountain grassland
Subalpine

Figure 6. Palaeovegetation maps for Georgia, 14,000 to 1,000 cal. yr BP, based on TWINSPAN ordination of radiocarbon-dated pollen data.

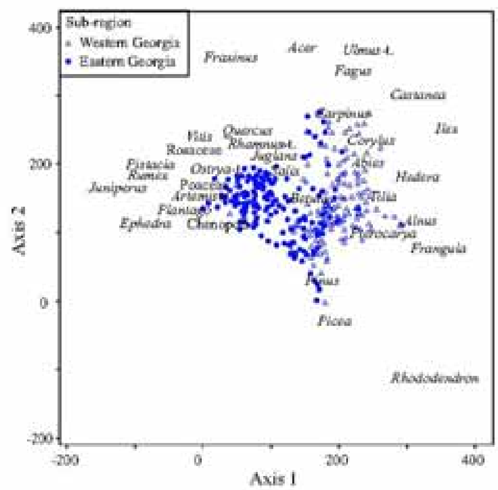


Figure 7. Detrended correspondence analysis (DCA) ordination of the Georgian pollen dataset. Sample scores are indicated by symbols, and taxa scores by taxa names.

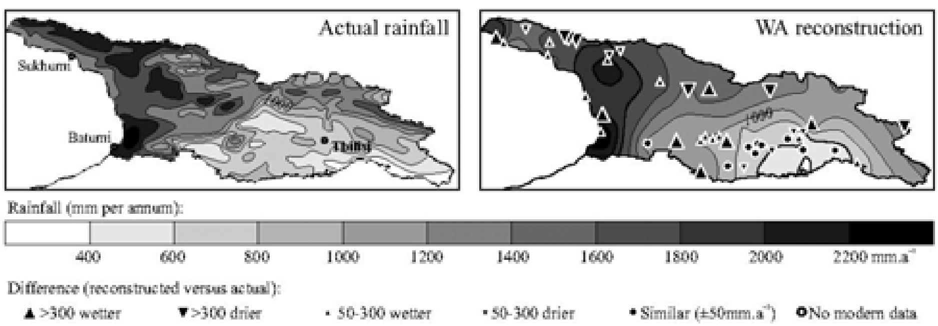


Figure 8. Actual rainfall pattern in Georgia compared to the pollen-based reconstruction extrapolated from study sites. Arrows indicate differences

between actual and reconstructed values. Present-day rainfall map based on Tatashidze (2000, p. 96).

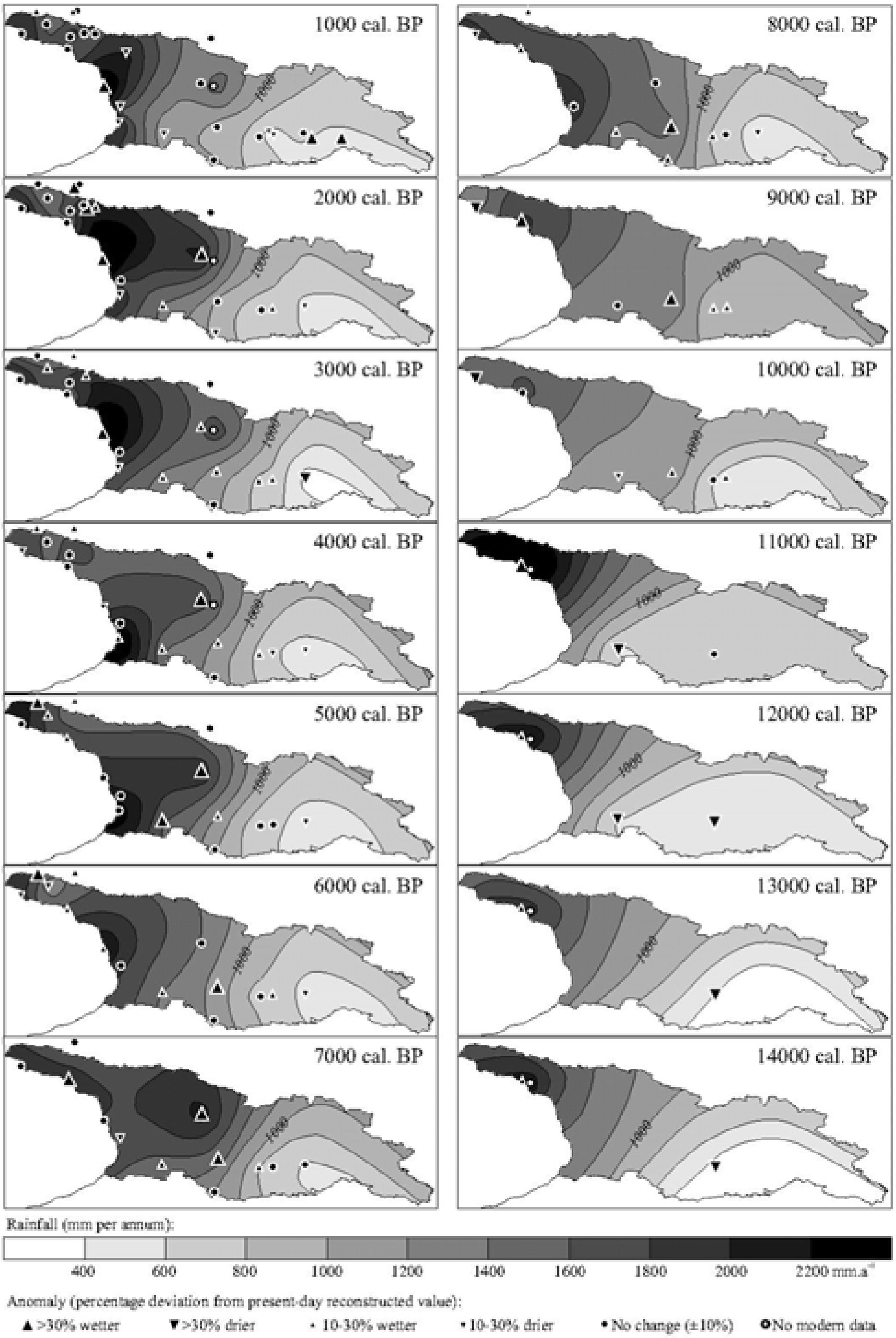

1000 cal. BP
2000 cal. BP
3000 cal. BP
4000 cal. BP
5000 cal. BP
6000 cal. BP
7000 cal. BP
8000 cal. BP
9000 cal. BP
10000 cal. BP
11000 cal. BP
12000 cal. BP
13000 cal. BP
14000 cal. BP
1000
Rainfall (mm per annum):
400
600
800
1000
1200
1400
1600
1800
2000
2200 mm.a⁻¹
Anomaly (percentage deviation from present-day reconstructed value):
▲ >30% wetter
▼ >30% drier
10-30% wetter
10-30% drier
No change (±10%)
No modern data

Figure 9. Reconstructed rainfall anomalies for Georgia, 14,000 to 1,000 cal. yr BP, generated using a WA transfer function. Anomalies (triangles) indicate differences between the past and present reconstructed values in percentage terms. Reconstructed values are shaded grey. These values pertain only to the study sites indicated; values extrapolated between sites should be viewed cautiously, as they take no account of bioclimatic variation.

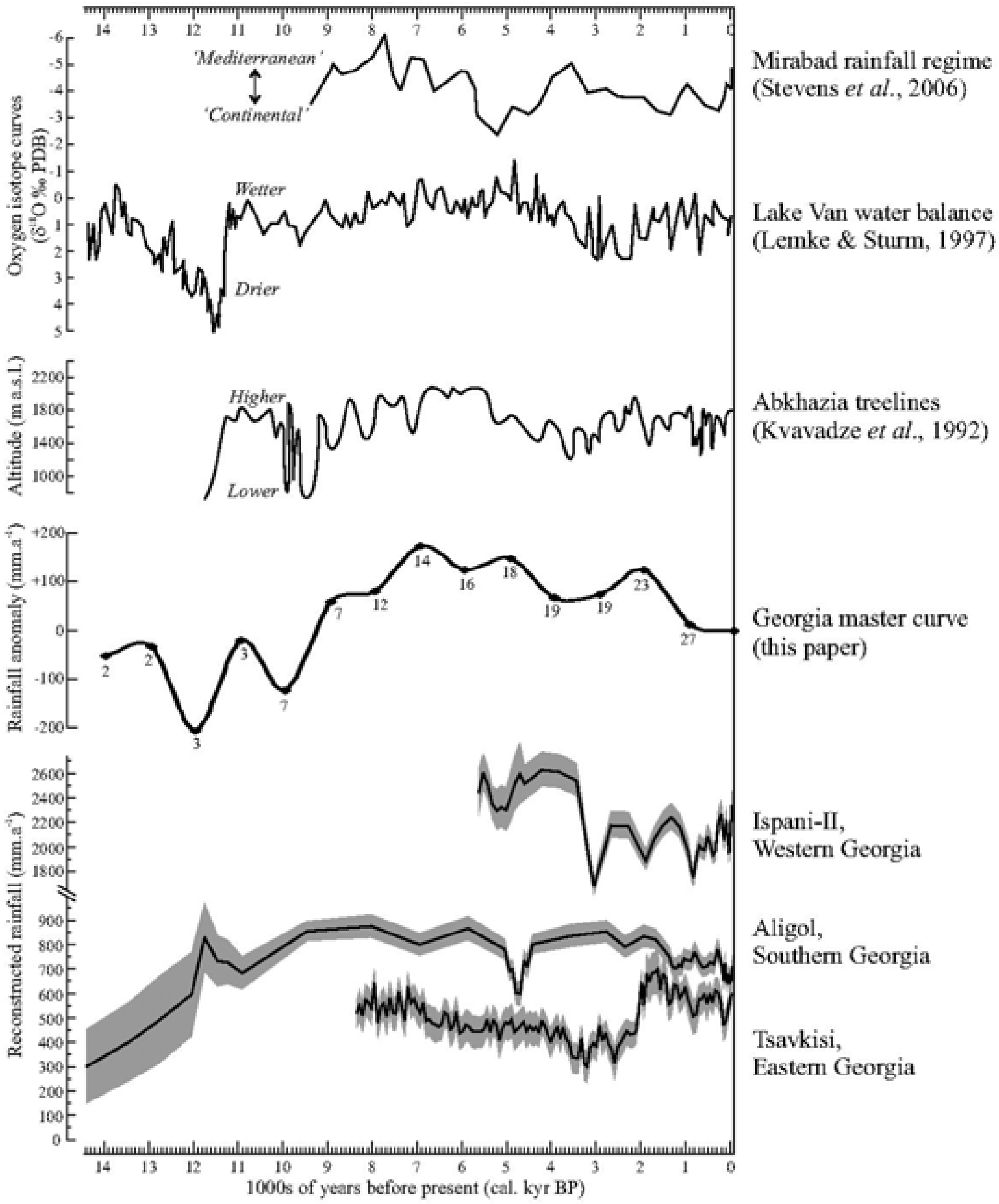


Figure 10. Comparison of some late Quaternary palaeoclimatic trends from Western Asia. The bold line is the Georgian master curve, produced by applying the transfer function to all data from sites in Figure 1. Numerals next to the curve indicate the number of sites used to derive the average rainfall anomaly. The upper section of the diagram shows the oxygen isotope curves from Lake

Mirabad (Iran) and Lake Van (Turkey), as well as a pollen-based treeline scheme for Abkhazia. Interpretations of these curves are indicated. Curves in the lower part of the diagram are local rainfall trends produced by applying the transfer function to pollen data from three contrasting sites in Georgia (see text). Grey-shaded areas depict standard errors.

TABLES

Table 1. Study sites at which the pollen-based reconstruction of Georgia's vegetation (using TWINSPAN) fails to match the observed vegetation exactly.

Site and sample no.	Pollen-based vegetation	Observed vegetation
Lagodekhi 6	Oak-xerophyte	Subalpine (above mixed forests)
Cherepanov 2-3	Mountain grassland	Oak forest, mountain grassland
Imnati core top	Mixed forest	Alder swamps, some mixed forest
Lisi 2	Mixed forest	Mountain grassland, semidesert-steppe
Lagodekhi 1, 2, 4, 5	Mixed forest	Subalpine (above mixed forests)
Urukh 109, 111	Alder swamp-forest	Mixed and conifer forest (N Caucasian)
Akhaltsikhe 183	Conifer forest	Mountain grassland
Ktsiis Zeda Vake	Conifer forest	Mountain grassland
Nariani	Conifer forest	Mountain grassland
Kartsakhi	Conifer forest	Mountain grassland

Table 2. Pollen taxa most strongly correlated with each axis of the DCA ordination of Georgian pollen data. Correlation coefficients (r^2) are given in parentheses.

Axis 1 + *Alnus* (0.48)

	–	Poaceae (0.61), Chenopodiaceae (0.47), *Artemisia* (0.43), *Quercus* (0.38)
Axis 2	+	*Fagus* (0.45), *Carpinus betulus* (0.27), *Ulmus-Zelkova* (0.26)
	–	*Pinus* (0.54), *Picea* (0.24)
Axis 3	+	*Picea* (0.30), *Fagus* (0.23)
	–	*Alnus* (0.54)

Table 3. Performance statistics for rainfall reconstruction models produced by the modern analogue technique (MAT) and weighted averaging (WA). RMSEP – root-mean-squared error of prediction.

	MAT	WA
R^2	0.80	0.77
Cross-validated R^2	0.78	0.72
RMSEP ($mm.a^{-1}$)	316	314
Duplicate data R^2	0.45	0.55

PHOTO CAPTION

Dawn at Mt Kazbegi (5034 m), Caucasus Mountains. Greek legend tells us that Zeus shackled Prometheus to this, Georgia's highest peak, for stealing fire from the gods. Prometheus' torment was to have an eagle peck out his liver each day. One may feel some empathy for the Greek titan after being treated to the wine-soaked hospitality that welcomes every visitor to this land of extraordinary beauty and cultural riches (photo: Simon Connor).