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A survey of modern pollen and vegetation along an altitudinal transect in southern Georgia, Caucasus region.

Simon E. Connor[a*], Ian Thomas[a], Eliso V. Kvavadze[b], Giorgi J. Arabuli[c], Genia S. Avakov[b] and Antonio Sagona[d]

[a]*School of Anthropology, Geography and Environmental Studies, University of Melbourne, VIC 3010, Australia*

[b]*Institute of Paleobiology, Georgian Academy of Sciences, Niagvris kucha 4a, Tbilisi 380004, Georgia*

[c]*Botanical Department, State Museum of Georgia, Georgian Academy of Sciences, Rustavelis gamziri 3, Tbilisi 0105, Georgia*

[d]*School of Art History, Cinema, Classics and Archaeology, University of Melbourne, VIC 3010, Australia*

Abstract

This paper describes the pollen representation of vegetation patterns along an altitudinal transect in the South Caucasus region. Surface sediments from eight small- to medium-sized lakes and wetlands were analysed for modern pollen and the results analysed numerically using detrended correspondence analysis (DCA) and dichotomised ordination (TWINSPAN). Pollen spectra from the semidesert region have a clear palynological signal characterised by an abundance of Chenopodiaceae. Differentiation of oak forest, upper tree-line and subalpine communities is more difficult: all are dominated by arboreal pollen types. The authors propose a number of indicator pollen types and pollen threshold values that may assist in detecting tree-line variations and deforestation events in Holocene pollen diagrams.

Keywords

pollen; vegetation; climate; tree-lines; numerical analysis; Caucasus

[*] Corresponding author. Fax: +61 3 83444972; e-mail: s.connor@pgrad.unimelb.edu.au

1. Introduction

The discrimination of forested and open vegetation types is a necessary prelude to any palaeoecological interpretation that aims to identify tree-line variations and deforestation events in fossil pollen spectra.

Traditionally, pollen representation studies have made use of moss polster or surface soil samples and related these to the surrounding vegetation (Bradshaw, 1981; Bunting, 2002; Davis, 1980; Elliot, 1999; Gajewski et al., 2002; Islebe and Hooghiemstra, 1995; Paez et al., 2001; Tinsley and Smith, 1974; Vermoere et al., 2000; Wright et al., 1967). Several of these have previously been undertaken in the Caucasus region, using soil or moss samples collected over long altitudinal transects (Klopotovskaya, 1973; Kvavadze, 1993; Kvavadze, 1999; Kvavadze and Efremov, 1994; Kvavadze and Efremov, 1995; Stuchlik and Kvavadze, 1995; Yazvenko, 1991). However, the application of these studies to the interpretation of fossil pollen diagrams is limited by the fact that few sites used in palaeoenvironmental reconstructions have a comparable source area to soil or moss samples (Hicks, 2001; Kvavadze and Efremov, 1995). Consequently, pollen indicators derived from soil samples and moss polsters cannot be strictly applied to the interpretation of lake and wetland sediments.

Moss polsters beneath forest canopies are dominated by pollen originating in approximately the surrounding 20-30m, small forest hollows by pollen from 50-100m, whilst sediments at the centre of large lakes may have pollen spectra dominated by a regional component derived from a source area of perhaps many hundreds of kilometres (Andersen, 1970; Calcote, 1995; Jacobson and Bradshaw, 1981; Janssen, 1966; Prentice, 1985; Sugita, 1993).

These source area concepts are based on conditions in northern hemisphere temperate forests and may not apply to research in areas where semidesert steppes, deforested foothills and upland grasslands are characteristic vegetation types (Davies and Fall, 2001). Study sites within open landscapes have a greater potential pollen source area than those in a closed-canopy forest due to the removal of the trunk space (Tauber, 1965) or gravity component (Jacobson and Bradshaw, 1981) and the absence of filtration by arboreal vegetation (Tauber, 1967). Upland sites are typically dominated by arboreal pollen generated by lowland forests (Fall, 1992; Frei, 1997; Haberle and Bennett, 2001; Islebe and Hooghiemstra, 1995; Kvavadze, 1993; Markgraf, 1980) and determining the position of tree-lines palynologically is therefore difficult and potentially flawed (Birks and Birks, 2000).

In mountainous regions, conifer stomate analyses have shown that arboreal pollen percentages and influx rates rise as forests advance toward a study site, and often decline once forests are present *in situ* (Ammann and Wick, 1993; David, 1997; Pisaric et al., 2000). Human activity may also result in a greater influx of forest tree pollen, increasing arboreal pollen percentages during deforestation events (Aaby, 1988). The relationship between arboreal pollen abundance and forest abundance is therefore non-linear.

In the semi-arid regions of the Caucasus, differentiation of open *versus* forested conditions in late-Quaternary pollen diagrams is crucial in contextualising a rich archaeological record. Hence, this paper asks: can open and forested environments in Georgia be differentiated using modern pollen data; and, if so, are there indicator pollen specific to certain plant communities?

2. Study area

Georgia is a nation bordered by mountains (Fig. 1). To the country's north, the anticlinal Greater Caucasus Mountains rise to a maximum elevation of 5642m a.s.l. (Mt Elbrus); and to the south lie the volcanic Anticaucasus Uplands.

Within our study area of the Anticaucasus, the Samsari and Javakheti Ranges (Fig. 2) reach a maximum elevation of 3300m (Mt. Didi Abuli). These upper-Pliocene/Quaternary basaltic and andesitic ridges (Maisuradze, 1989) run perpendicular to the dominant west-to-east storm tracks originating over the Black Sea, creating a rain shadow in eastern Georgia. Annual rainfall varies from approximately 800mm on the Javakheti Range to less than 400mm in the steppic lowlands near the Georgian capital, Tbilisi (SSSR, 1964). May is generally the wettest month, and January the driest. Annual average winter temperatures vary considerably in the study region, from –10°C in the mountains to 0°C in the lowlands (abs. min. –28°C), and 14 to 25°C in summer (abs. max. 40°C) (SSSR, 1964; Tatashidze, 2000).

The soils of the lowlands overlie Quaternary pluvio-glacial and alluvial sediments. Solonchak soils occur in enclosed synclinal depressions in the semideserts. Skeletal and peaty soils are found in alpine areas (such as the Javakheti and Samsari ridges), shallow greyish soils in the upper forest belts on basalt substrates, chestnut and brown forest soils on foothill slopes, and chernozems in both semidesert and subalpine areas (Berg, 1950; Gregory and Shave, 1944).

The vegetation of eastern Georgia (Fig. 2) falls broadly into the Irano-Turanian group (Zohary, 1973). Semideserts and lowland steppes are dominated by Poaceae-Chenopodiaceae-*Artemisia* associations, with patches of arid open woodland

including *Pistacia mutica, Celtis caucasica, Pyrus salicifolia, Amygdalus georgica, Rhamnus pallasii, Juniperus* spp.*, Ephedra procera* and *Cotinus coggygria* (Dolukhanov, 1966; Nakhutsrishvili, 1999). Lower tree-line vegetation communities are highly human-impacted, corresponding broadly to Mediterranean 'garrigue' and 'maquis'. Most are former oak or oak-hornbeam woodlands that have been subjected to continuous deforestation and burning (Avakov, 1982; Badenkov et al., 1990), leading to a proliferation of fire- and herbivore-tolerant species such as *Paliurus spina-christi*.

The east Georgian forest belt (Fig. 2) is constricted by low rainfall, steep topography and human impact. Mixed broadleaf *Quercus-Carpinus* forests are dominant from the foothills to the anthropogenic upper tree-line and replaced by fragments of *Fagus orientalis*-dominated forest on moist north-facing slopes. Disjunct pockets of *Pinus kochiana* exist in rocky gorges and on steep slopes, and are thought to represent remnants of its greater distribution during glacial times (Gulisashvili, 1949). Forests of *Picea orientalis* and *Abies nordmanniana* are rare under the continental climatic regime of eastern Georgia, occurring only along the ridgeline of the Trialeti Range (Fig. 2).

Subalpine vegetation of the Tsalka and Javakheti volcanic plateaux consists of species-rich steppic grasslands dominated by *Festuca ovina, Bromus* spp., *Koeleria cristata, Poa alpina, Nardus stricta, Carex* spp. and others (Magakian, 1933). Human impact in the subalpine region is especially pronounced, under the combined effects of cattle grazing, deforestation and hay-making (Badenkov et al., 1990; Bock et al., 1995).

3. Methods

We selected eight lakes and wetlands along an altitudinal transect running across southern Georgia from lowland steppe-semidesert to subalpine environments (Fig. 2, Table 1).

Sites include a semidesert salina (Sakhare Tba), a lowland salt lake (Kumisis Tba), a wetland at the steppe-forest ecotone (Tsavkisis Tba), a lake within oak-hornbeam forest (Cherepanovis Tba), a small mire at the upper tree-line (Trialetis Tba), two maar lakes on the subalpine Tsalka Plateau (Imeras Tba and Baretis Tba), and a bog on the treeless Javakheti Plateau (Avchalagöl). Fluvial input into all sites is absent or minimal.

We calculated forest area values in Table 1 with reference to Sugita's model for an entire lake surface (Sugita, 1993) and forest data on 1:100000 topographic maps. To account for differences in pollen sizes, we found it useful to approximate the model by defining the 50% pollen source radius as ten times the basin radius. This weights our calculated source area from 'relatively light' to 'relatively heavy' pollen types (Sugita, 1993) such as *Quercus, Carpinus, Fagus* and *Pinus*, these being predominant in the region's forests.

At Sakhare, Tsavkisi, Cherepanovi, Trialeti and Imera, the surrounding vegetation was described and percentage aerial cover estimates were made using the Domin scale. As the layering of vegetation at forest sites produced total cover percentages in excess of 100%, the forest area values (Table 1) were applied, enabling pollen percentages and vegetation percentages to be compared semi-quantitatively.

Plant nomenclature follows Czerepanov (1995).

Surficial lake and wetland sediments were sampled to provide source-area analogues to aid the interpretation of Holocene pollen records from the same sites. Three to four samples, each comprising a composite of sediment gathered over a 5 x 5m area, were collected from each site to achieve a representative coverage. In addition, moss polsters and surface soils were collected at the oak-hornbeam forest site for comparative purposes.

Individual surface samples were homogenised before extracting 1cm^3 samples for pollen analysis. Two *Lycopodium* marker spore tablets (University of Lund, batch 938934) were added prior to processing. Pollen extraction involved carbonate removal in 10% HCl, boiling in KOH, heavy liquid separation in Sodium polytungstate (Hart, 1988), HF treatment to digest fine silica, and acetolysis to remove dispersed organics (Moore et al., 1991). Samples were mounted in glycerol and pollen identified using type material held at the University of Melbourne and published pollen keys (Bobrov et al., 1983; Chester and Raine, 2001; Kuprianova and Aleshina, 1972; Kuprianova and Aleshina, 1978; Moore et al., 1991). Most samples were counted to a minimum of 400 terrestrial pollen grains. Charcoal fragments were quantified using the point-count method (Clark, 1982). Pollen diagrams were drawn in Psimpoll (Bennett, 2002).

Percentage pollen data were analysed using a variety of multivariate numerical methods. Only dryland taxa found in more than two samples were included in the analyses.

Weighted-averaging methods proved satisfactory as they allow for unimodal responses to environmental gradients (ter Braak and Prentice, 1988). Detrended correspondence analysis (DCA)(Hill and Gauch, 1980), a form of indirect gradient analysis, was executed using the debugged version of DECORANA (Hill, 1979a;

Oksanen and Minchin, 1997) in Psimpoll 4.10 (Bennett, 2002). Rescaled DCA was performed on all taxa, with rare types downweighted. The results were checked with non-metric multidimensional scaling (*sensu* Ejrnæs, 2000) and the gradients appear to be robust.

Two-way indicator species analysis (TWINSPAN) (Hill, 1979b) was run on untransformed data in PC-ORD 4.25 (McCune and Mefford, 1999). This divisive classification method is less sensitive to the background 'noise' created by regional pollen than some other techniques. TWINSPAN produces a series of dichotomies based on a reciprocal averaging ordination similar to DCA. Samples are split into two groups at each division, based on their position on the ordination axis. At each split, the pseudospecies (quantitative presence/absence measure of a species) that best differentiates the two groups is given as an indicator. TWINSPAN indicators have considerable value for ecological interpretation and classification of the resulting groups. The maximum number of pseudospecies cut levels was selected, and rare types downweighted manually.

4. Results and discussion

Pollen proportions of major taxa are shown in relation to altitudinal, vegetational and climatic gradients in Figure 3a/b. The taxa are arranged according to their order in the TWINSPAN table so that the associations between, for example, Chenopodiaceae and Polygonaceae in the semidesert-steppe spectra, are apparent.

The TWINSPAN clusters and group numbers (shown in Figure 3b) show that the semidesert-steppe spectra (TWINSPAN group 3) are clearly differentiated from spectra where pollen of forest trees are more prevalent (TWINSPAN group 2). The

analysis also differentiates between pollen spectra from forest sites (TWINSPAN group 19) and treeless subalpine sites (TWINSPAN group 18).

The species that best describes the difference between these and other groups is given as a TWINSPAN indicator, shown in Table 2. This means that TWINSPAN group 18 can be distinguished from TWINSPAN group 19 by *Picea* proportions greater than 1.5%. Within TWINSPAN group 19, the oak-forest group (39) can be split from the upper tree-line group (38) by the presence of more than 2% *Cerealia*-type pollen in the former, and the representation of *Capsella bursa-pastoris* and *Polygonum aviculare*-type pollen in the latter.

Pollen data are discussed in relation to the vegetation and climate of the three major landscape units (semidesert-steppe, forest and subalpine) in the sections below:

4.1. Lowland steppes and semideserts of Gareji and Lower Kartli (TWINSPAN groups 7, 6 and 10)

Along the altitudinal transect, pollen spectra (Fig. 3a/b) show a clear response to climatic gradients (Fig. 3a). This is particularly evident in the relationship between Chenopodiaceae pollen proportions and annual rainfall.

In other parts of the Near East, Chenopodiaceae:*Artemisia* (C/A) ratios have been used to estimate aridity levels from pollen data (Davies and Fall, 2001; El-Moslimany, 1990). In our study area, however, C/A ratios show a relatively poor relationship to rainfall (r^2=0.34) compared to Chenopodiaceae percentages alone (r^2=0.81). This may be related to the application of C/A ratios to lake sediments rather than soils, or the different ecology of *Artemisia* in the Caucasus. *Artemisia* pollen is more common in TWINSPAN group 6 (approx. 350mm. annual rainfall) than

group 7 (approx. 400mm. annual rainfall), and is a TWINSPAN indicator of the former (Table 2).

In the study region, *Artemisia fragrans* is found in desert/semidesert vegetation communities, which were, until the mid-20th Century, relatively widespread on the arid lowlands and foothills of the eastern Caucasus (Dolukhanov, 1966). Semidesert vegetation formerly occupied areas suitable for cotton and grain agriculture, and its present distribution is relatively fragmentary, occurring mainly on saline soils (Dolukhanov, 1966).

Although a semidesert community, dominated by *Artemisia fragrans* and *Salsola nodulosa*, exists on the lake terrace of Sakhare Tba (site S, TWINSPAN group 7), it appears that the pollen representation of Chenopodiaceae is much greater than *Artemisia* (Table 3) and the various members of the Poaceae family. Amongst these, *Festuca valesiaca* and *Stipa pulcherrima* are dominant in the arid steppe grasslands, which are used for cattle grazing and are burnt frequently by herders to encourage fresh grass growth and restrict reestablishment of woody plants. High charcoal concentrations in the sediments (Fig. 3b) may reflect these burning practices. *Polygonum aviculare*-type and other Polygonaceae pollen are common in the pollen spectra, although we could not locate source plants in the surrounding vegetation.

Consistent with the predominantly-treeless landscape of the semideserts and arid steppes (Fig. 4), arboreal pollen (AP) occurs in small proportions, except in sediments from the centre of saline lake, Kumisis Tba (TWINSPAN group 10 – forest-steppe), where AP reaches 23%, compared to 2% in samples taken nearer the lake edge (TWINSPAN group 6 – semidesert-steppe). Source-area differences are thought to explain this intra-basin AP variation.

4.2. Forests of south-eastern Georgia (TWINSPAN groups 11, 38 and 39)

The forest cover of the eastern slopes of the Anticaucasus Mountains in Georgia is little-studied and poorly-described (Prof. R. Gagnidze, Director, Botanical Institute, Georgian Academy of Sciences, pers. comm.). Both the lower and upper tree-lines are anthropogenic (Ketskhoveli, 1959), posing particular problems for identifying tree-line analogues in modern pollen spectra and climatic shifts in fossil pollen spectra.

The forest belt is dominated by mixed broadleaf tree associations, in which *Quercus iberica, Carpinus caucasica, C. orientalis* and *Fagus orientalis* predominate. At the steppe-forest ecotone near Tsavkisis Tba (Site Ts, TWINSPAN group 11), the dominant forest type is *Carpinus orientalis-Quercus iberica*, and although this forms a majority of the site's surrounding vegetation, it is very poorly represented in the pollen spectra (Table 4) when compared to *Pinus* pollen. Pine plantations occupy approximately 20% of the wetland's calculated pollen source area. Apple orchards occupy a similar area, but are palynologically 'silent'. TWINSPAN indicators include pollen of cultivated trees (*Populus, Pinus* and *Cedrus*) and *Plantago lanceolata*, an anthropogenic indicator (Behre, 1986).

Chenopodiaceae pollen proportions are lower than in the steppe-semidesert sites, consistent with the higher rainfall received by this site (approx. 500mm *per annum*). And, despite the relatively forested catchment (60%), arboreal pollen proportions average only 27%, of which *Pinus* pollen contributes over half.

Similarly, within the forest belt proper (Cherepanovis Tba, site C, TWINSPAN group 39), AP averages only 35%. Sugita *et al.* (1999) have suggested that arboreal pollen *versus* non-arboreal pollen (AP:NAP) ratios are ineffective in determining

landscape openness from pollen data, and our results confirm this. There is no relationship between AP:NAP ratios and forest cover values in this study (r^2=0.0001).

The forests surrounding Lake Cherepanovis Tba are dominated by *Quercus iberica* and *Carpinus caucasica*, with a shrubby understorey dominated by members of the Rosaceae (Table 5). Small fragments of pure *Fagus orientalis* forest (Fagetum nudum) are found on moist, north-facing slopes. Polydominant forests are common in the region, in which, along with the above species, *Acer campestre, A. laetum, Carpinus orientalis, Cerasus avium, Crataegus curvisepala, C. pentagina, Fraxinus excelsior, Populus tremula, Pyrus caucasica, Ulmus glabra* and other trees are more-or-less common. Above 1450m. elevation, mountain oak (*Quercus macranthera*) begins to replace the Georgian oak (*Quercus iberica*) in *Quercus-Carpinus caucasica* associations. In clearings, such as the lake terrace of Cherepanovis Tba (Fig. 5), meadow vegetation dominated by *Agrostis planifolia* and other grasses may be found.

Table 5 shows the relationship between vegetation composition and the pollen spectra of lake sediments from Cherepanovis Tba, moss polsters from the forest floor, and soil samples from the same forest. The pollen spectra of the lake sediments are dominated by Poaceae and *Quercus* (AP: 35%), the moss polster spectra by *Quercus, Carpinus caucasica* and *Pinus* (AP: 67%), and the soil sample spectra by *Pinus*, Chenopodiaceae and *Quercus* (AP: 43%). These significant differences in the pollen spectra highlight the difficulties in using soil samples and moss polsters as modern analogues for lake sediment pollen records.

The TWINSPAN indicator for these oak-forest samples is *Cerealia*-type pollen (Table 2). The nearest agricultural land is a considerable distance from the site, so the prevalence of cereal pollen may relate to the presence of wild cereals in the area. The Caucasus is regarded as a centre of wild cereal diversity (Vavilov, 1992), and some of

these were harvested by Neolithic populations (Kiguradze, 1986). Hillman (1996) has proposed that domestic cereals were selected from wild varieties found in *Quercus*-Rosaceae 'parklands'. *Quercus* and *Cerealia*-type pollen percentages are positively-correlated in samples from this study (r^2=0.44).

The upper tree-line site (Trialetis Tba, site Tr, TWINSPAN group 38) is an infilled maar lake situated directly above the Khrami River Canyon. Immediately adjacent the site is a *Quercus iberica* and *Q. macranthera* forest (on the southern slope), a secondary forest dominated by *Corylus avellana, Carpinus caucasica* and *Fraxinus excelsior* (on the northern slope), and a diverse subalpine meadow (Table 6). Forest area at this site is approximately 45%, and AP levels vary between 17 and 20%.

Corylus is greatly underrepresented in the pollen spectra: it is the dominant canopy tree in the secondary forest, but contributes to less than 5% of the AP sum. *Pinus* and *Quercus* are the dominant AP taxa, and the site is differentiated from the oak-forest site by the selection of the open vegetation indicators, *Polygonum aviculare*-type and *Capsella bursa-pastoris* (*Hornungia*-type), as TWINSPAN indicators (Table 2).

In the forest sites, charred particles (Fig. 3b) are constantly represented in sediments. Each site has an area of open grassland nearby that may be contributing this micro-charcoal, or it may derive from *in-situ* burning of the wetland vegetation.

4.3. Subalpine steppic grasslands of the Tsalka and Javakheti Plateaux (TWINSPAN groups 8, 36 and 37).

With the exception of TWINSPAN group 8, discussed below, the subalpine sites (Imeras Tba, Baretis Tba and Avchalagöl) form subgroups 36 and 37 of TWINSPAN

group 18, indicated by *Picea* proportions greater than 1.5% (Table 2). This contrasts with the forest groups, where *Picea* pollen is present only in trace proportions.

Picea orientalis is found in 'dark coniferous forests', common on the moist western slopes of the Anticaucasus Mountains (Nakhutsrishvili, 1999). On the drier eastern slopes (the study area), the distribution of *Picea orientalis* is extremely restricted, and the quantities of *Picea* pollen found in the subalpine sediments studied here can only be the result of long-distance pollen transport. Previous work in the Anticaucasus (Margalitadze, 1995) suggests that *Picea* pollen percentages are approximately equal to *Pinus* percentages where *Picea orientalis*-dominated forests are present *in situ*.

Pinus is the dominant AP taxon and AP percentages reach their highest levels (up to 63%) along the entire altitudinal gradient. Pollen taxa such as *Pterocarya, Buxus, Zelkova, Olea europaea, Ephedra distachya*-type, *E. fragilis, Pistacia* and *Hippophaë* indicate significant long-distance pollen transport from lowland sources over 100 kilometres distant. *Corylus* pollen is more abundant in the sediments of Imeras Tba (site I, TWINSPAN group 37) than in the tree-line site adjacent growing populations of *Corylus avellana*, a particular problem for the interpretation of fossil pollen spectra.

Another problem is the importance of several members of the Poaceae family in the especially diverse wetland vegetation of Imeras Tba (Table 7), and the absolute dominance of grasses in the treeless subalpine steppes of the study region. Any change in either steppe or wetland vegetation will affect Poaceae pollen proportions, so interpretation of landscape openness in the fossil context must rest on other subalpine herbs and forbs.

Fire is a significant human impact in the subalpine rangelands of the Anticaucasus and the mountainous regions of north-eastern Anatolia. Shepherds and cattle herders intentionally burn large tracts of the subalpine plateaux each October in order to promote fresh grass in the following spring. The subalpine grassland and some of the wetland vegetation around Imeras Tba had been burnt when we visited in 2002 (Fig. 6). The charcoal concentrations in the sediments (Fig. 3b) are surprisingly low given this fact, and must relate to the low intensity of the burns, or to the retention of charcoal fragments in the wetland fringe vegetation.

In contrast, the sediments of Avchalagöl are exceedingly rich in charred particles. A significant area of this shallow, *Carex*-dominated wetland had been burnt in late-2001. The two samples obtained from the burnt sections of the wetland are comprised in TWINSPAN group 8, indicated by an absence of *Ranunculus*-type pollen and increased proportions of *Fraxinus* (Table 2). Pollen of several late-flowering species present in the unburnt sections are lacking in the burnt sections, i.e: *Ranunculus*-type, *Cichorium*-type, *Galium*-type and Brassicaceae.

4.4. Pollen Representation

The relationship between vegetation and modern pollen spectra of several study sites is shown quantitatively in Tables 3-7. Based on these data, it appears that *Pinus* and *Quercus* are high pollen producers and are always well represented in pollen spectra. *Fagus* and *Carpinus caucasica* are moderate pollen producers, *Carpinus orientalis* and *Corylus* are relatively-poor pollen producers, and *Fraxinus* and Rosaceae are very poor. These observations are in accord with the representation factors calculated by Andersen (1970). Of the above taxa, *Pinus, Corylus* and *Fraxinus* are probably best dispersed, due to their lightweight pollen grains. As a

result, these pollen types can be expected in most pollen spectra, regardless of their proximity to source plants.

The pollen representation of herbaceous plants appears to depend largely upon their pollination strategy. Wind-pollinated genera, such as Poaceae and Polypodiaceae, are well represented, whereas insect-pollinated Scrophulariaceae, Boraginaceae, Caryophyllaceae and Fabaceae are generally under-represented in pollen spectra. Others, such as the Chenopodiaceae, Plantaginaceae and Polygonaceae, are over-represented, occurring in almost all pollen spectra but in few vegetation surveys.

Because the use of AP:NAP ratios is unsuitable for differentiating forested and open vegetation types from pollen data in the study region, the 'background' pollen level must be estimated (Sugita et al., 1999). This is illustrated in Figure 7, which shows selected proportions of tree pollen calculated from the AP sum along the entire altitudinal transect. *Pinus* pollen comprises up to 35% of arboreal pollen even when it is absent from the extra-local vegetation; 35-50% when it is found nearby; and over 50% when it is present and locally-dominant.

Quercus is locally present and dominant when its AP proportions exceed 30%; nearby or sub-dominant at 15-30%; and at background level below 15%. Difficulties arise when applying this method to *Carpinus caucasica, Fagus* and *Corylus*. These taxa are co-dominant in the forests of the region, but have a poorer pollen representation than *Pinus* and *Quercus*. A two-step procedure is required to determine whether these species are local or regional. Firstly, a background level of approximately 20% for *Carpinus caucasica* and *Fagus*, and 5% for *Corylus* can be adopted based on the regional thresholds in Figure 7. Percentages approaching these thresholds can then be compared to other AP taxa. Where *Quercus* is either 'nearby'

or 'local', and *Pinus* is 'absent', then we may assume that *Carpinus caucasica / Fagus / Corylus* are present in the local vegetation or dominant extra-locally.

These preliminary thresholds are approximate, and should be applied to fossil pollen spectra with a degree of caution as not all vegetation associations were sampled, and background levels may have varied through time in response to human impacts and climate change. For example, the establishment of extensive *Pinus* plantations in the past fifty years may have elevated background levels of *Pinus* pollen.

4.5. Environmental gradients

The relationship between annual rainfall and Chenopodiaceae pollen percentages has already been discussed, but additional environmental gradients were identified by Detrended Correspondence Analysis (DCA). These are shown in Figure 8(a) as vector lines. Since DCA uses the same chi-squared dissimilarity coefficient as TWINSPAN, the results can be discussed in terms of the TWINSPAN groups.

DCA Axis 1 is correlated with annual rainfall (r^2=0.82), elevation (r^2=0.79), summer temperature (r^2=0.72) and longitude (r^2=0.68). The correlations with winter temperature (r^2=0.49), summer rainfall (r^2=0.48) and winter rainfall (r^2=0.33) are weaker. The results suggest that prediction of temperature and rainfall should be possible from pollen data, although a data-set gathered from a larger spatial area would be desirable before this is done, because rainfall and temperature are auto-correlated in this analysis.

Correlations with the second axis include winter rainfall (r^2=0.41), the charred particle : dryland pollen concentration (CP:DLP) ratio (r^2=0.22) and percentage forest cover (r^2=0.22). The latter is particularly important, as the forests (TWINSPAN groups

38, 39) are undifferentiated from the subalpine steppes (groups 8, 36, 37) in terms of rainfall and elevation on Axis 1. The second axis shows that forested landscapes may be distinguished from open subalpine steppes on the basis of pollen spectra.

The relationship between winter rainfall and the forest belt (TWINSPAN groups 38 and 39) is also noteworthy. In winter, dominant north-westerly winds carry moisture over the Trialeti Range to the forest sites. In summer, the generally calmer wind regime oscillates between moist northwesterlies and dry southeasterlies (SSSR, 1964). Wind trajectories are such that the forested slopes intercept orographic winter rain, whereas the flat subalpine plateaux (TWINSPAN groups 8, 36, 37) receive less.

The relationship between the TWINSPAN groups and some individual pollen taxa is shown in Figure 8(b). Semidesert and arid steppes (groups 6, 7, 8) are characterised by pollen spectra rich in Chenopodiaceae, Polygonaceae and *Polygonum aviculare*-type. TWINSPAN group 10, with its large source area, occupies a place between these and the forest-steppe ecotone group (11), where *Juniperus, Pinus, Cedrus, Plantago lanceolata* and Polypodiaceae are important.

The forest belt (38, 39) is characterised by the importance of *Quercus* in pollen spectra, and the presence of *Carpinus orientalis, Crataegus*-type, *Acer, Cerealia*-type, *Sanguisorba officinalis, Plantago media*-type, *Cirsium, Ranunculus*-type and Caryophyllaceae. The subalpine groups (8, 36, 37) are characterised by the representation of their TWINSPAN indicator, *Picea*, and numerous other taxa: *Betula, Pinus, Corylus, Fraxinus, Rumex, Sanguisorba minor, Dipsacus/Cephalaria, Filipendula, Polygonum bistorta,* Apiaceae, Brassicaceae, etc.

The results suggest that these taxa may have indicator value in determining landscape openness from pollen data, regardless of the under-representation of

arboreal pollen in forests and its over-representation in subalpine grasslands. The CP:DLP ratio is also associated with open sites (Fig. 8a), and charred particle analysis may provide a further proxy of landscape openness in regions where grasslands are subject to periodic anthropogenic burning and forest fires are relatively rare.

5. Conclusion

This paper demonstrates that climatic gradients and landscape openness can be determined from the pollen spectra of lake and wetland sediments. Previous studies in the Caucasus (Kvavadze, 1993; Stuchlik and Kvavadze, 1995) noted the inherent difficulty in distinguishing between upland open and forested sites through pollen data. In the mountains, where winds of high velocity and duration are responsible for long-distance pollen transport, and where local pollination is often entomophilous, the use of AP:NAP ratios is of little value in quantifying landscape openness.

Instead, we suggest a slightly more complex approach, based on the presence and abundance of indicator pollen types, distinctions between regional background pollen rain and local pollen production, and the use of charred particle analysis.

This procedure remains to be tested against other sites, plant communities and fossil records, but provides a strong starting-point for a more quantitative approach to pollen-based vegetation reconstructions in the South Caucasus region.

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Table 1. Site locations and associated environmental variables. See text for an explanation of forest area calculations. Type: L- lake site, W- wetland site.

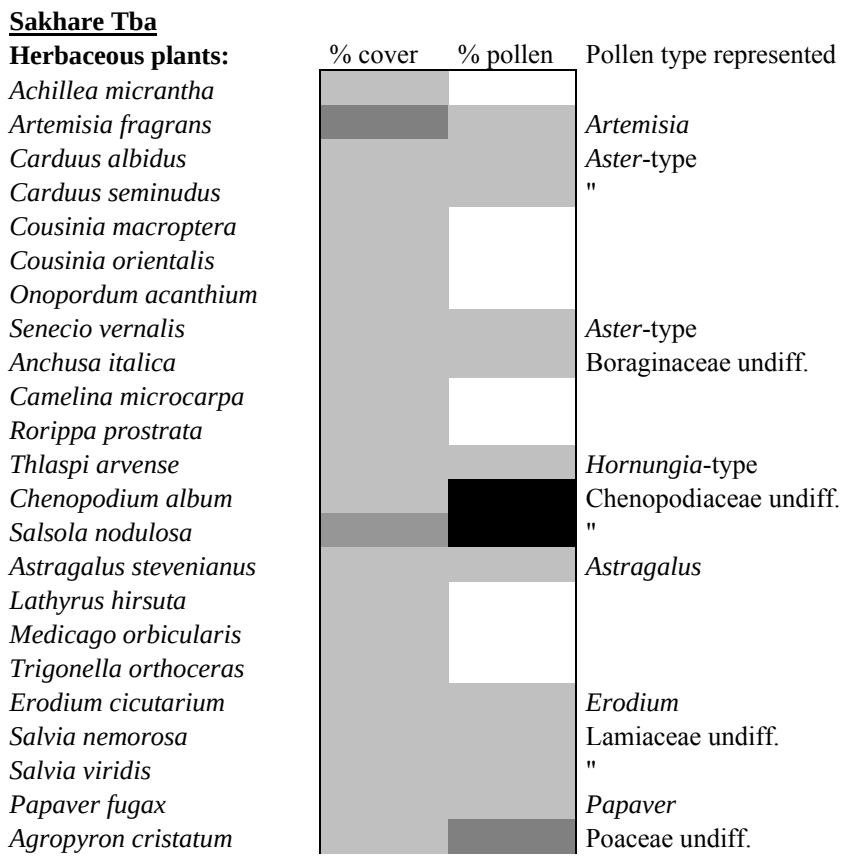
Site code	Site name	Type	Location (Lat.; Long.)	Elevation (m a.s.l.)	Basin avg. radius (m)	Forest area (%)	Vegetation type
S	Sakhare tba	W	41°35′N; 45°19′E	800	190	0	Semidesert/steppe
K	Kumisis tba	L	41°35′N; 44°50′E	469	1070	<1	Semidesert/steppe
Ts	Tsavkisis tba	W	41°41′N; 44°45′E	1100	100	60	Steppe/forest
C	Cherepanovis tba	L/W	41°34′N; 44°22′E	1400	210	70	Mixed forest
Tr	Trialetis tba	W	41°32′N; 44°07′E	1520	140	45	Upper tree-line
I	Imeras tba	L/W	41°39′N; 44°12′E	1600	140	0	Subalpine steppe
B	Baretis tba	L/W	41°39′N; 44°10′E	1620	620	<5	Subalpine steppe
A	Avchalagöl	W	41°20′N; 43°42′E	2050	417	<1	Subalpine steppe

Table 2. Positive ‘perfect’ indicators for TWINSPAN groups in Figure 3b. Each indicator occurs only in that group at the stipulated level. Groups not included in the table have no positive TWINSPAN indicators, hence an absence of the indicator of the opposite group may be used.

TWINSPAN group	Ecological interpretation	TWINSPAN indicators and their cut levels
2	Forest and upland	*Quercus* 1%; *Pinus* 2, 3%
5	Steppe-forest	Chenopodiaceae 10%; *Populus* >0%

6	Lowland steppe	*Artemisia* 2%; *Aster*-type 0.5, 1%; Lamiaceae 2%; *Juglans* >0%
7	Semidesert/steppe	Primulaceae 1.5%
8	Subalpine (burnt)	*Fraxinus* 2%
9	Subalpine and forest (unburnt)	*Ranunculus* >0%
11	Steppe-forest	*Cedrus* >0%; *Pinus* 5, 10%; *Picea* 0.5%; Poaceae 10%; *Plantago lanceolata* >0, 0.5, 1%
18	Subalpine steppe	*Picea* 1.5%
37	Subalpine steppe	*Fagus* 5%; *Quercus* 5%; *Carpinus caucasica* 5%
38	Upper tree-line	*Polygonum aviculare* >0, 0.5, 1%; *Capsella bursa-pastoris* >0%
39	Oak forest	*Cerealia*-type 2%

Table 3. Plant community composition and pollen spectra at semidesert site Sakhare Tba (Site S). The table compares the cover abundance ('% cover') of plant species to the abundance of corresponding pollen types ('% pollen'), the values indicated by shading (see legend). Blank spaces indicate that no corresponding pollen types were found. Inverted commas (") indicate that the pollen taxon represents several of the plant species listed, e.g: Poaceae pollen represents *Agropyron, Alopecurus, Bromus* and other grasses.



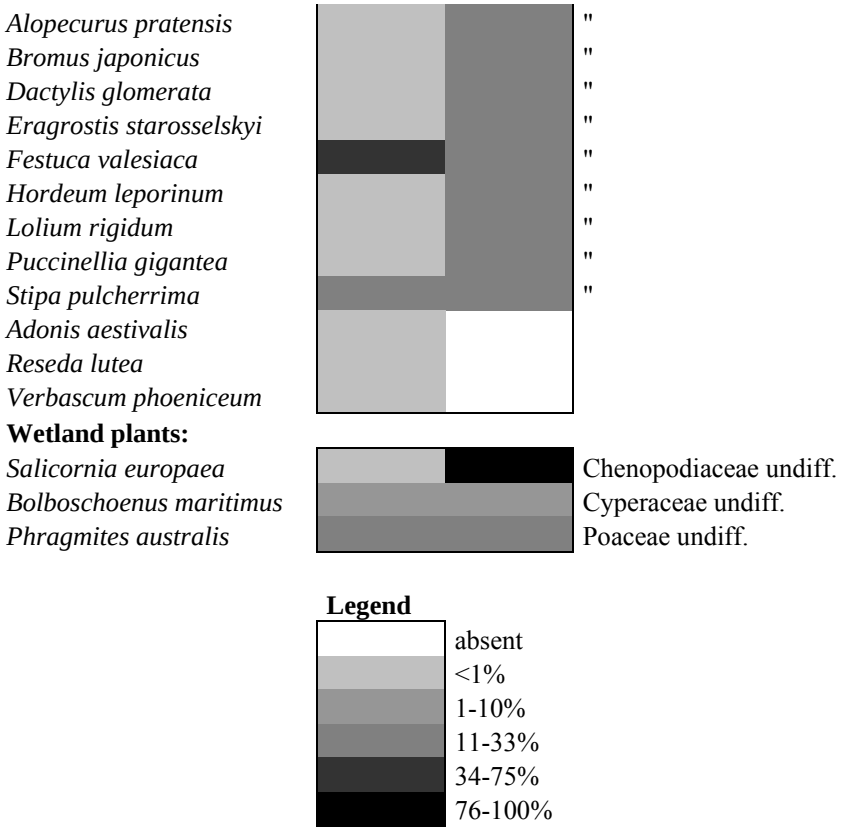
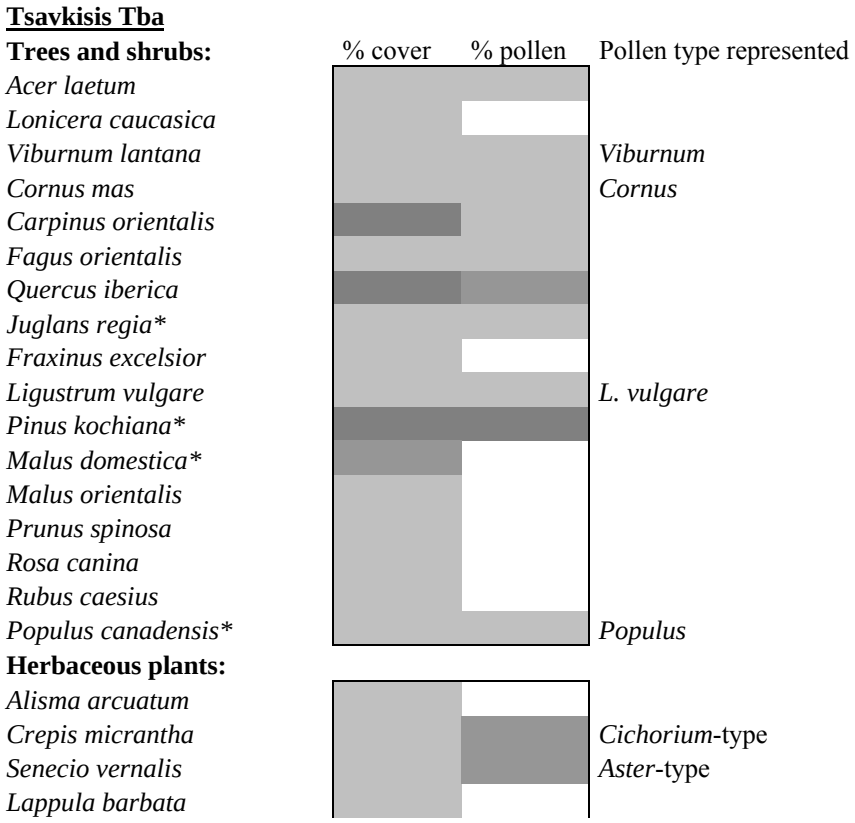
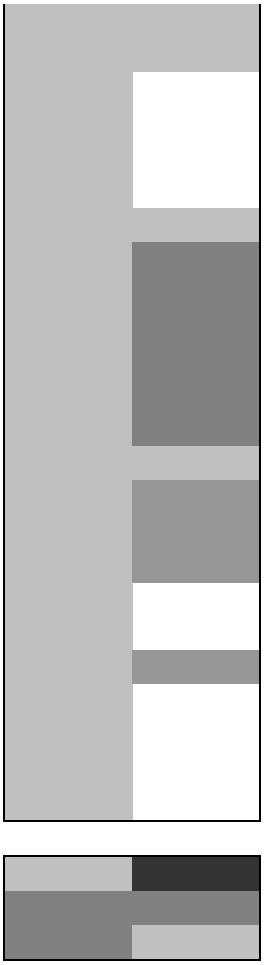


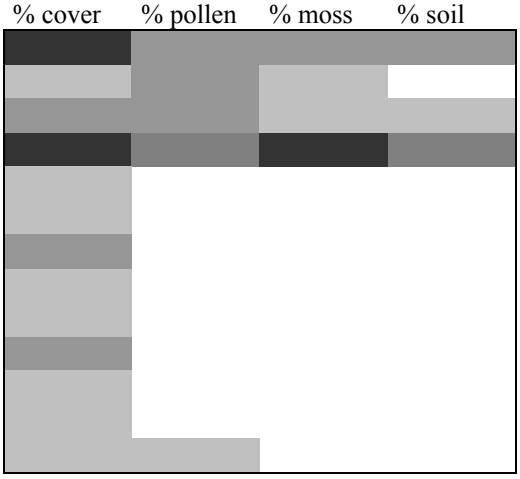
Table 4. Plant community composition and pollen spectra at lower tree-line site Tsavkisis Tba (Site Ts). See Table 3 for explanation and legend.





Hesperis matronalis	Brassicaceae undiff.
Campanula collina	*Campanula*
Silene viscosa	
Euphorbia helioscopia	
Astragalus viciifolius	
Onobrychis transcaucasica	
Scutellaria galericulata	Lamiaceae undiff.
Aegilops cylindrica	Poaceae undiff.
Bromopsis riparia	"
Koeleria cristata	"
Melica picta	"
Melica taurica	"
Nardurus krausei	"
Rumex acetosella	*Rumex*
Asplenium trichomanes	Polypodiaceae undiff.
Polypodium vulgare	"
Polystichum braunii	"
Trollius ranunculinus	
Geum urbanum	
Asperula arvensis	*Galium*-type
Digitalis ferruginea	
Veronica jacquinii	
Veronica serphyllifolia	
Hyosciamus niger	
Wetland plants:	
Carex vesicaria	Cyperaceae undiff.
Phragmites australis	Poaceae undiff.
Typha latifolia	*Typha*

Table 5. Plant community composition and pollen spectra at oak-hornbeam forest site Cherepanovis Tba (Site C). Pollen spectra of various media are compared: "% pollen" refers to pollen spectra of lake sediments, "% moss" to pollen spectra of moss polsters gathered in the nearby forest, and "% soil" to the pollen spectra of soil samples from the same forest. See Table 3 for additional explanatory notes.



Cherepanovis Tba					
Trees and shrubs:	% cover	% pollen	% moss	% soil	Pollen type represented
Carpinus caucasica					*C. caucasica*
Carpinus orientalis					*C. orientalis*
Fagus orientalis					*Fagus*
Quercus iberica					*Quercus*
Cerasus avium					
Crataegus curvisepala					
Crataegus pentagina					
Malus orientalis					
Prunus divaricata					
Pyrus caucasicus					
Rosa canina					
Populus tremula					
Salix caprea					*Salix*
Herbaceous plants:					

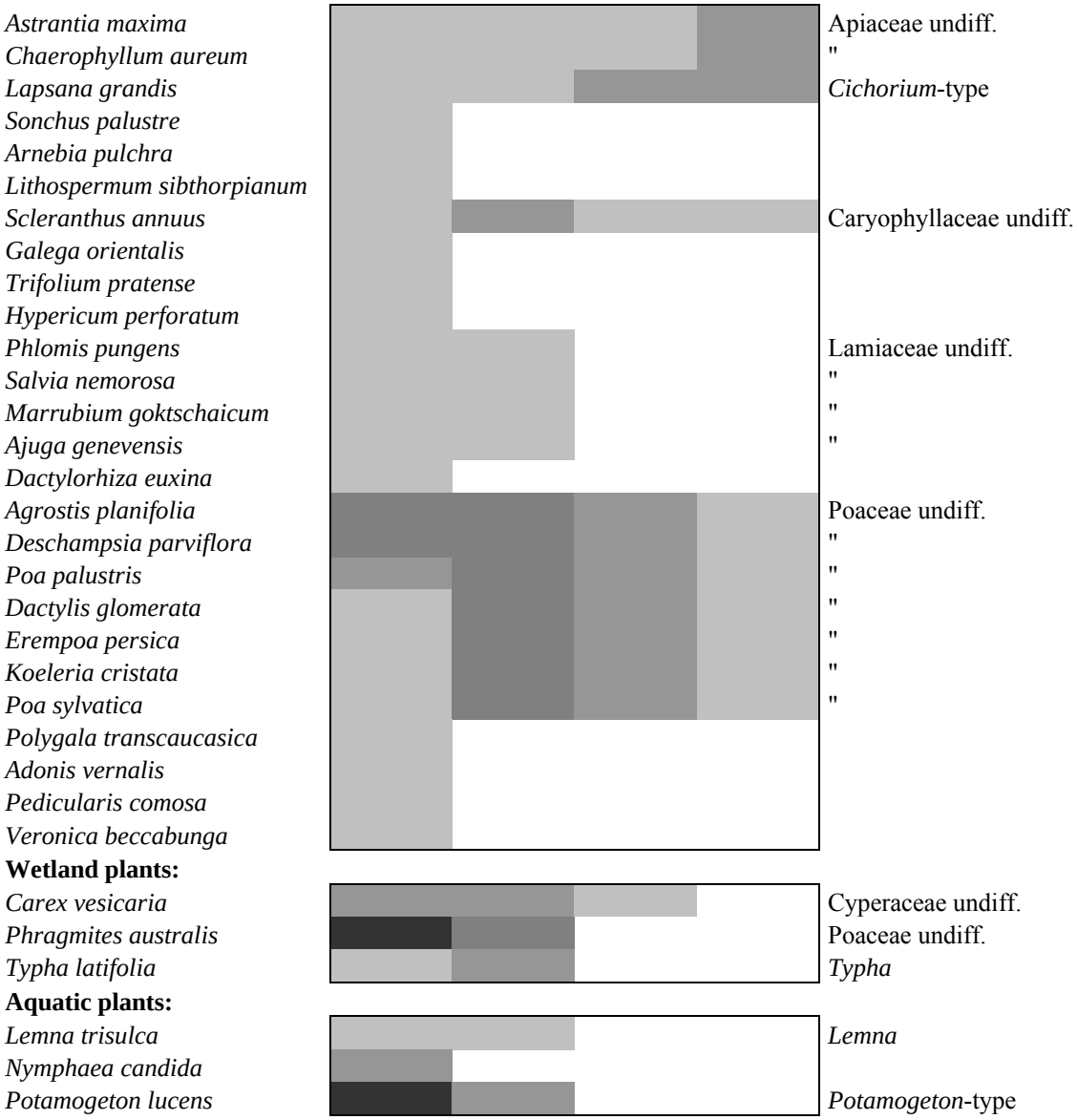
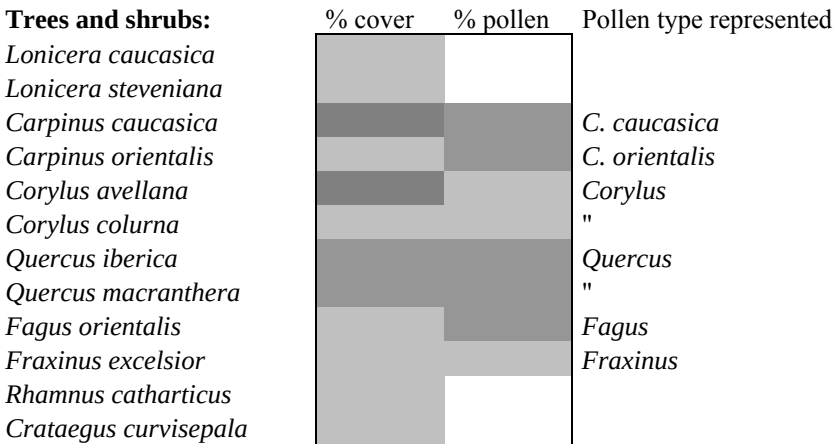
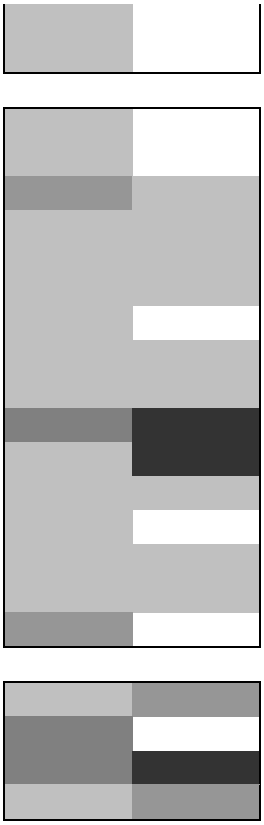


Table 6. Plant community composition and pollen spectra at upper tree-line site Trialetis Tba (Site Tr).

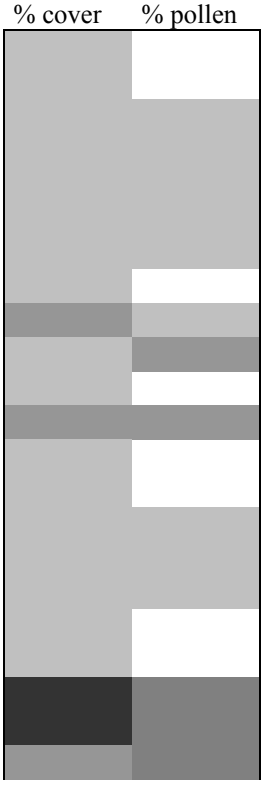
See Table 3 for explanation and legend.



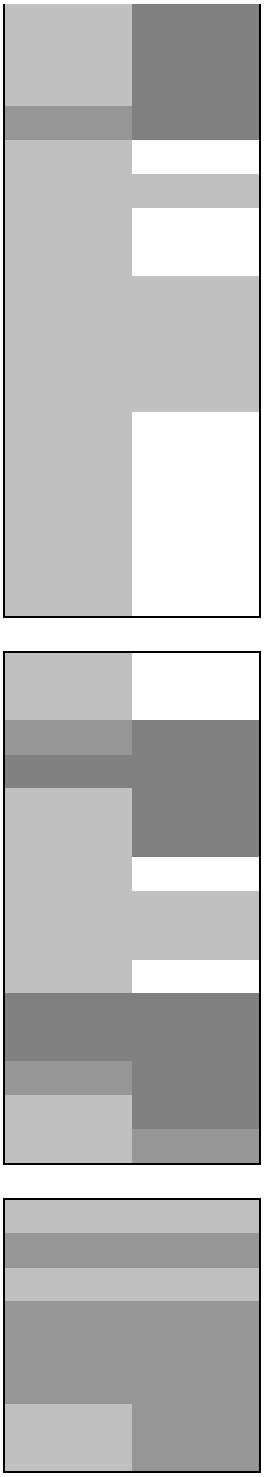


Rosa canina	
Sorbus boissierii	
Herbaceous plants:	
Sonchus palustris	
Pulmonaria dacica	
Capsella bursa-pastoris	*Hornungia*-type
Scleranthus annuus	Caryophyllaceae undiff.
Marrubium goktschaicum	Lamiaceae undiff.
Phlomis pungens	"
Asphodeline lutea	Liliaceae undiff.
Polygonatum verticillatum	"
Alopecurus sericeus	Poaceae undiff.
Bromopsis riparia	"
Dryopteris filix-mas	Polypodiaceae undiff.
Trollius ranunculinus	
Alchemilla valdehirsuta	*Alchemilla*-type
Asperula taurina	*Galium*-type
Veronica arvensis	
Wetland plants:	
Equisetum palustre	*Equisetum*
Juncus articulatus	
Phragmites australis	Poaceae undiff.
Potamogeton nodosus	*Potamogeton*-type

Table 7. Plant community composition and pollen spectra at subalpine steppic grassland site Imeras Tba (Site I). See Table 3 for explanation and legend.



Imeras Tba			
Herbaceous plants:	% cover	% pollen	Pollen type represented
Achillea setacea			
Arctium lappa			
Centaurea salicifolia			*Centaurea*
Cichorium intybus			*Cichorium*-type
Grossheimia macrocephala			*Centaurea phrygia*-type
Inula aspera			*Aster*-type
Taraxacum praticola			*Cichorium*-type
Anchusa gmelenii			
Capsella bursa-pastoris			*Hornungia*-type
Clypeola jonthlaspi			Brassicaceae undiff.
Erophila verna			
Scleranthus annuus			Caryophyllaceae undiff.
Cephalaria gigantea			
Euphorbia villosa			
Trifolium pratense			*Trifolium*-type
Vicia purpurea			Fabaceae undiff.
Vicia variabilis			"
Gentiana gelida			
Anacamptis pyramidalis			
Agrostis planifolia			Poaceae undiff.
Phleum phleoides			"
Phleum pratense			"



Dactylis glomerata	"
Deschampsia parviflora	"
Poa pratensis	"
Alopecurus aequalis	"
Polygala transcaucasica	
Rumex acetosella	*Rumex*
Trollius ranunculinus	
Alchemilla erythropoda	
Sanguisorba officinalis	*S. officinalis*
Asperula caucasica	*Galium*-type
Galium verum	"
Rubia tinctorum	"
Digitalis ferruginea	
Pedicularis comosa	
Pedicularis condensata	
Rynchocorys elephas	
Veronica anagallis-aquatica	
Viola montana	
Wetland plants:	
Alisma plantago-aquatica	
Sagittaria sagittifolia	
Carex dichroandra	Cyperaceae undiff.
Scirpus lacustris	"
Carex vesicaria	"
Juncellus pannonicus	"
Juncus effusus	
Mentha arvensis	*Mentha*-type
Stachys palustris	Lamiaceae undiff.
Epilobium hirsutum	
Phragmites australis	Poaceae undiff.
Scolochloa festucacea	"
Calamagrostis neglecta	"
Poa palustris	"
Typha latifolia	*Typha*
Aquatic plants:	
Myriophyllum spicatum	*Myriophyllum*
Nymphaea candida	*Nymphaea alba*-type
Polygonum amphibium	*P. amphibium*
Potamogeton gramineus	*Potomogeton*-type
Potamogeton lucens	"
Potamogeton natans	"
Sparganium minimum	*Sparganium*
Sparganium neglectum	"

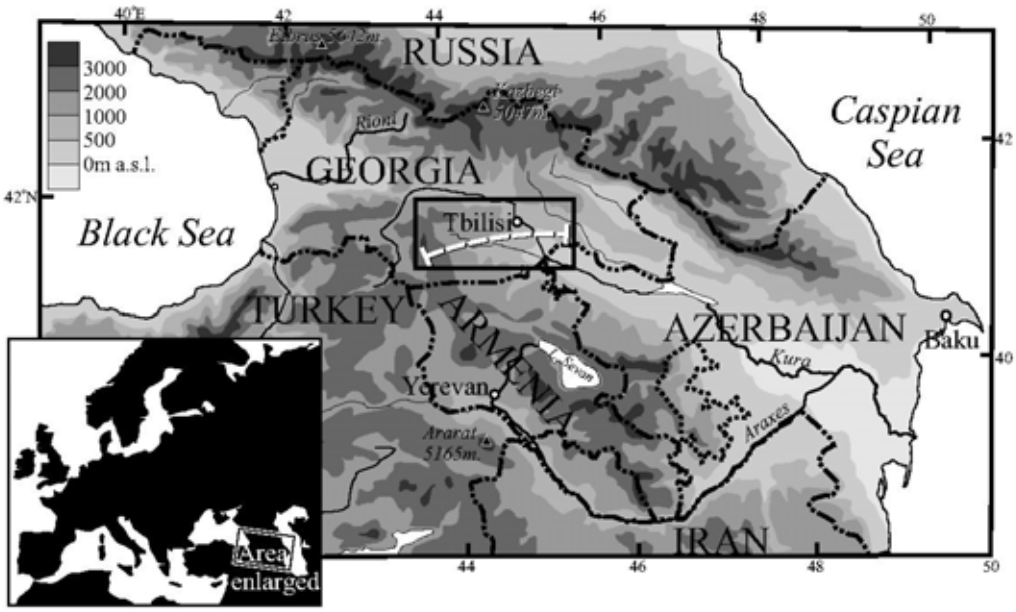


Figure 1. Topographic map of the South Caucasus region. Boxed area around Tbilisi indicates the study area enlarged in Fig. 2. The white dashed line indicates the position of the altitudinal transect shown in Fig. 3a.

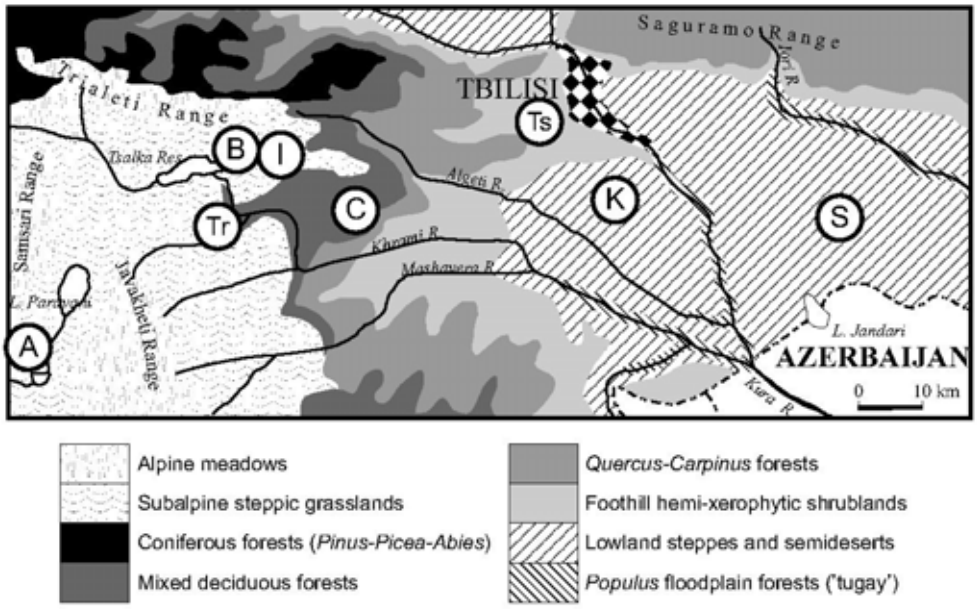


Figure 2. Map of principal vegetation types in the study area of southern Georgia, including study sites discussed in this paper. Site codes: S- Sakhare Tba, K- Kumisis Tba, Ts- Tsavkisis Tba, C- Cherepanovis Tba, Tr- Trialetis Tba, I- Imeras Tba, B- Baretis Tba, A- Avchalagöl. Adapted from SSSR Atlas (1964) and Ketskhoveli (1959).

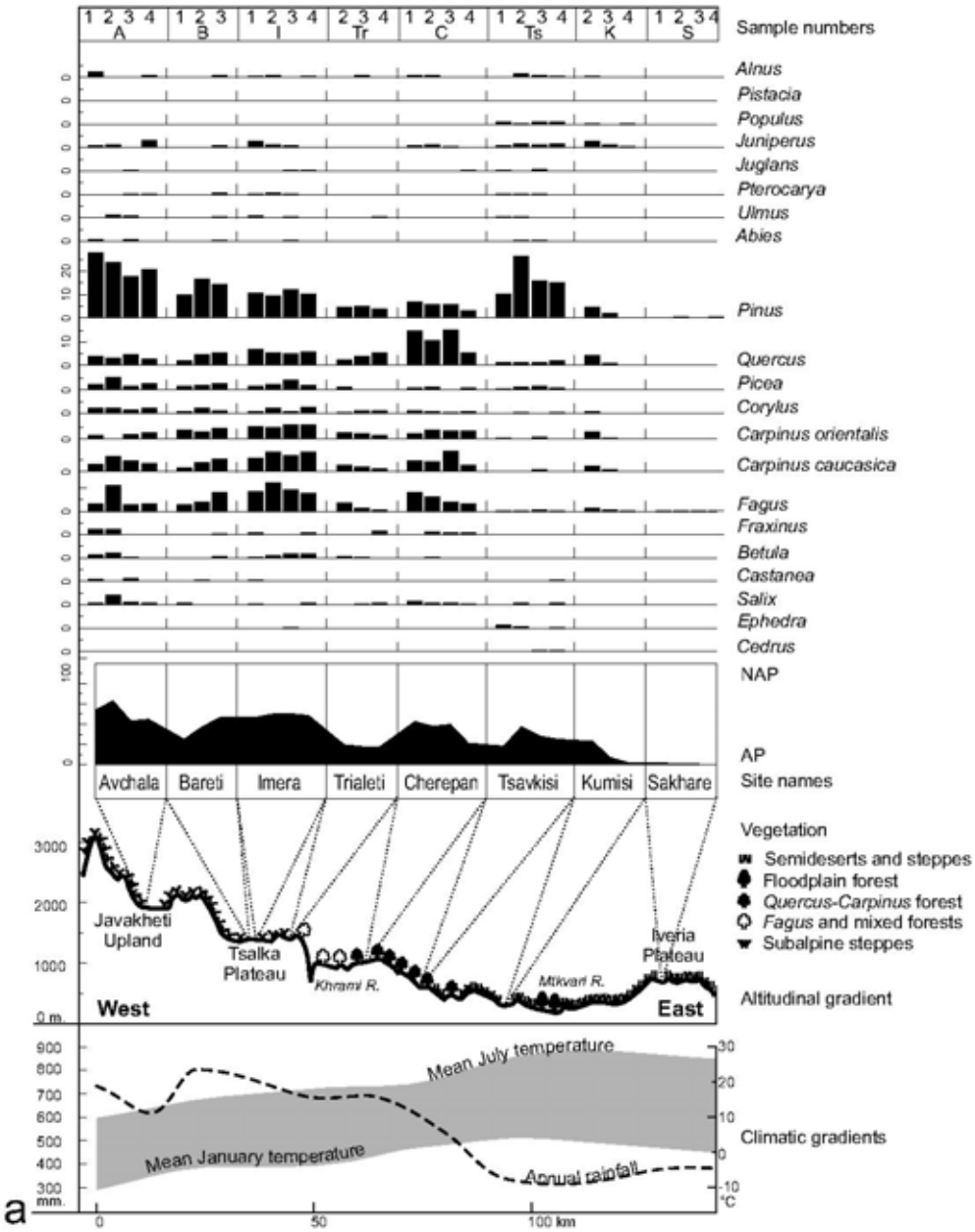


Figure 3(a). Diagram of altitudinal and climatic gradients, arboreal pollen (AP) to non-arboreal pollen (NAP) ratios and percentages of selected AP taxa calculated from the dryland pollen sum. Climatic data from SSSR (1964).

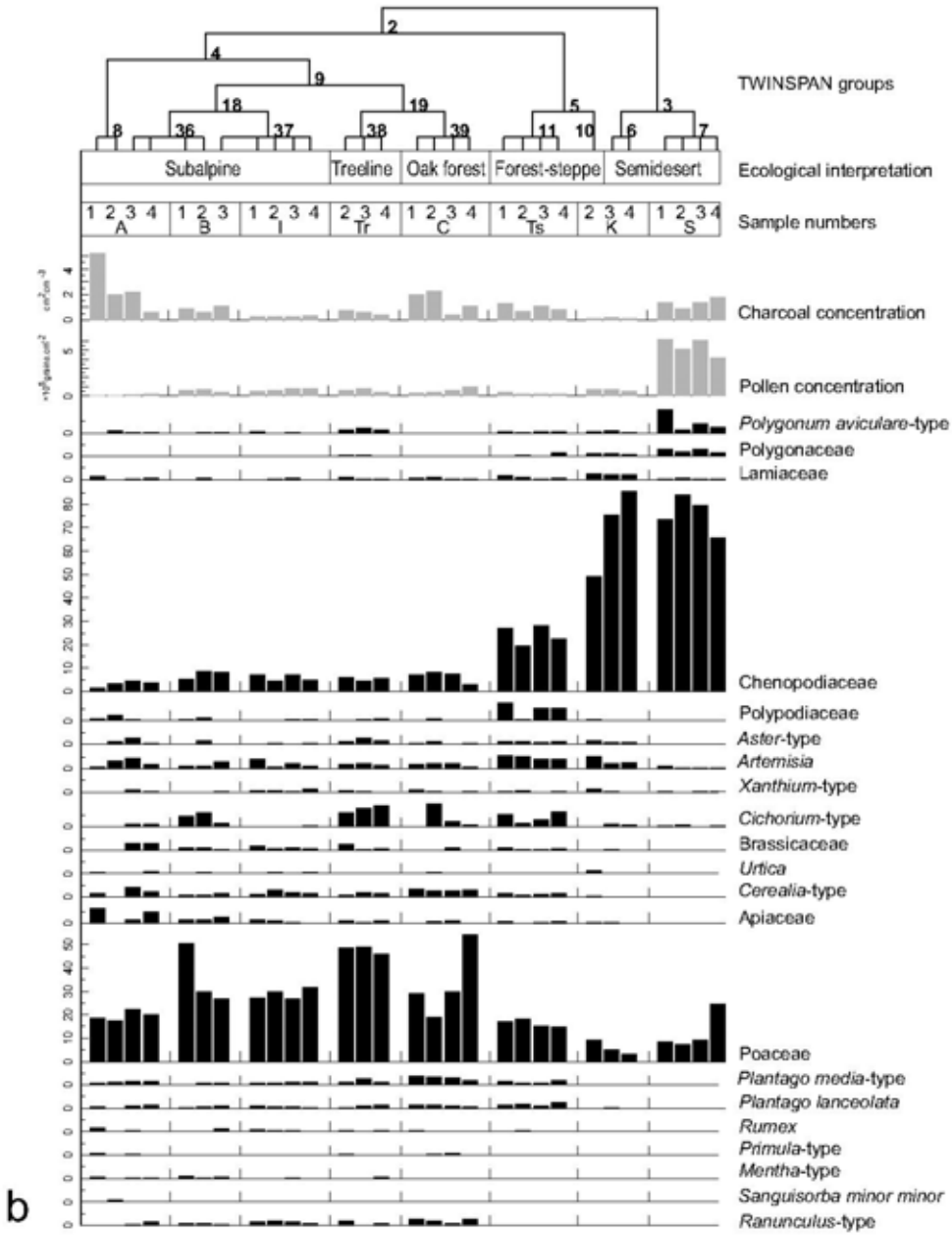


Figure 3(b). Diagram of percentages of selected non-arboreal pollen (NAP) taxa. Pollen and charcoal concentrations, and the results of two-way indicator species analysis (TWINSPAN) are shown at the top of the diagram. TWINSPAN indicators are provided in Table 2.

Figure 4. Photograph of the treeless steppes and semideserts of the Udabno-Gareji region, near Sakhare Tba (site S). In the foreground of the picture is the Davit Gareji monastery, founded in the 6th century A.D., where remnants of the forests that once covered the region can still be found.

Figure 5. Photograph of Cherepanovis Tba (site C) in the oak forest belt.

Figure 6. Photograph showing burnt hummocks of *Juncellus pannonicus* re-sprouting and flowering after a 2001 fire around the margins of subalpine lake Imeras Tba, Tsalka Plateau (site I).

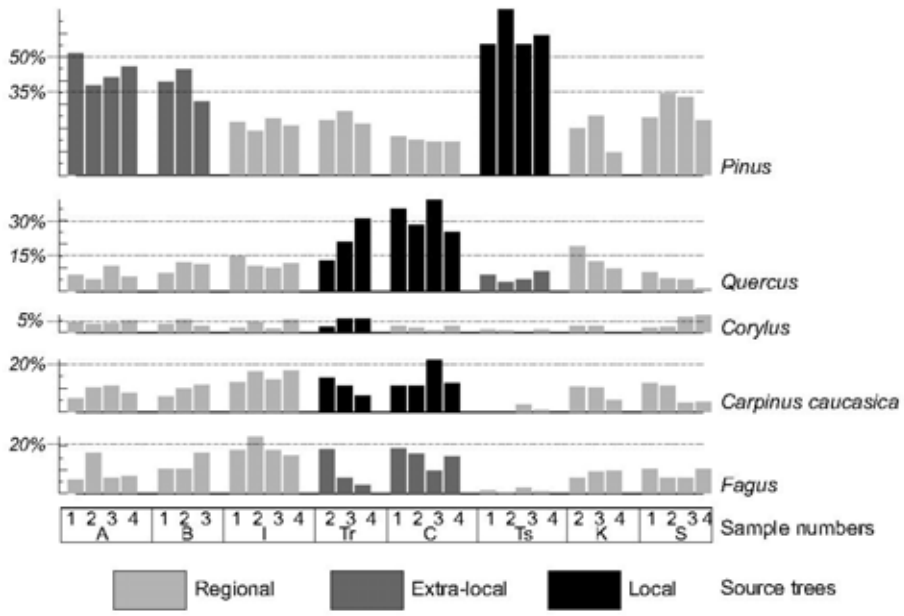


Figure 7. The pollen representation of the dominant forest trees of the study area, calculated from the arboreal pollen sum. Sample numbers follow Figure 3. Histogram bars are shaded according to each taxon's local, extra-local or regional occurrence in the vegetation around the sampling site, and the horizontal lines are the threshold values described in the text.

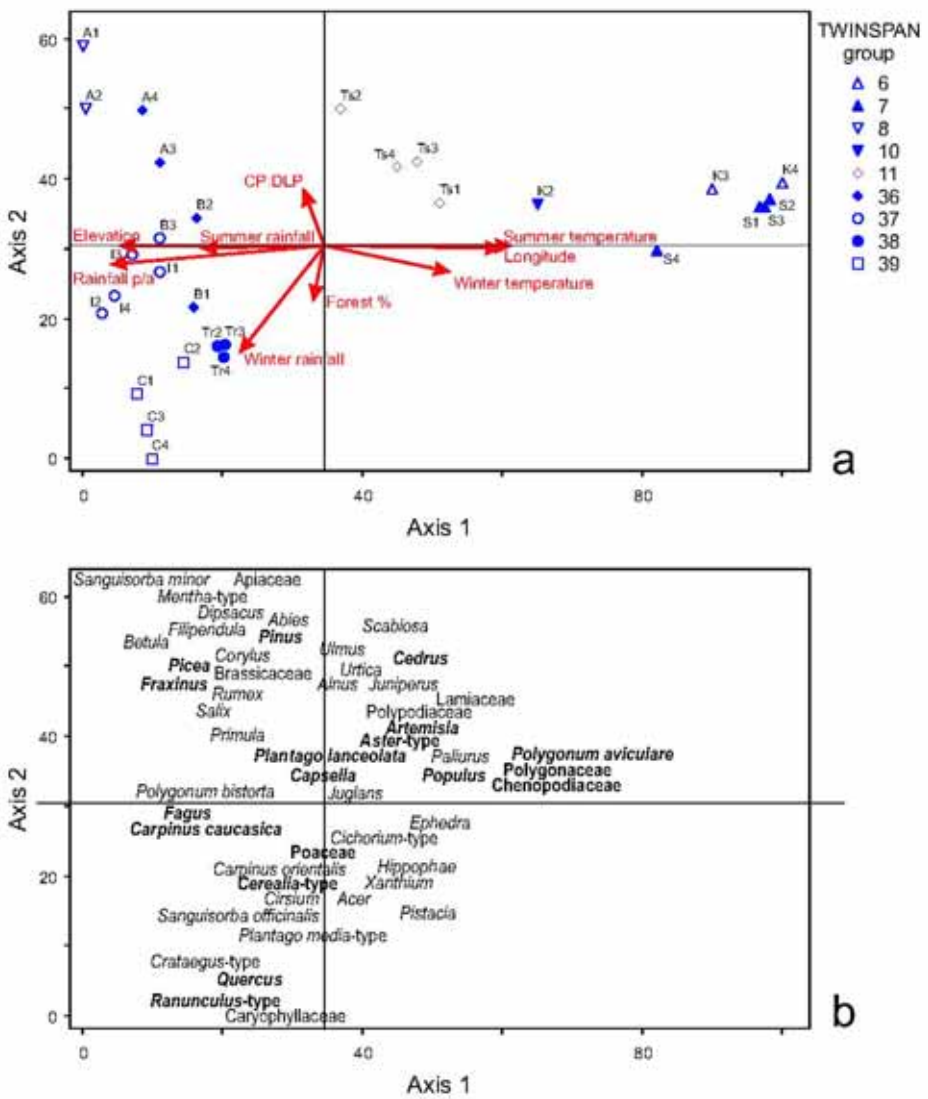


Figure 8(a). Detrended correspondence analysis (DCA) biplot of sample scores, TWINSPAN groups and correlated environmental variables (r^2 >0.2). Samples are labelled by site and sample number (see Fig. 3). CP:DLP refers to the charred particle to dryland pollen concentration ratio.

Figure 8(b). Weightings of selected pollen taxa in the DCA ordination space. Taxa in **bold type** are TWINSPAN indicators (see Table 2).

Author/s:

Connor, SE; Thomas, I; Kvavadze, EV; Arabuli, GJ; Avakov, GS; Sagona, A

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