Review of the Late Quaternary vegetation history of Epirus (NW Greece)

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Abstract. Based on data from the pollen analysis diagrams, an attempt has been made to represent in a synoptic manner the vegetation history of Epirus during the phases of Pleistocene and Holocene. In general, open steppe vegetation dominated during the glacial periods. Concurrently, though, forest vegetation was constantly present, especially in the mountainous regions of Epirus. Many woody species of the current temperate zone withdrew to and have survived in these regions. During the last interglacial, dense forest vegetation, which consisted mainly of mixed broadleaves, had developed, comprising many woody species that are now extinct. The vegetation development during the Early Holocene was influenced by the climate and resulted in the growth of forests in the plains as well as in the mountainous regions. Anthropogenic interference in Epirus has been traced back as early as the mid 6th millennium BC. Sooner or later, depending on the location, human interference, which mostly included pastoral activities, resulted in degradation and even extinction of the forest vegetation. Major events in the vegetation development of the last millennia were transformation of the deciduous oak forests to pseudomaquis or maquis vegetation mainly in the low and middle altitudes, and disappearance or withdrawal of the mountainous forest vegetation to lower altitudes, where forest limits have been formed as a result of human impact.

Key words: Epirus – Greece, Holocene, Pleistocene, pollen analysis, vegetation history

Introduction

Epirus is located in Northwest Greece. It is the most mountainous region of Greece, with a particularly intense and complex geomorphological anaglyph, starting from the Ionian Sea and ending at the Pindos mountain range. In combination with abundance of surface and ground waters associated with high precipitation, this anaglyph creates a plethora of alternating microenvironments and corresponding vegetation units of particular importance and interest.

In the western part of Epirus, starting from the seashore and up to 300–400 m a.s.l., the Quercetalia ilicis zone lies, dominated by phrygana and maquis. Above Quercetalia ilicis and up to 900 m, depending on the exposition, spreads the Quercetalia pubescentis zone. In the lower part of this zone (Ostryo-Carpinion orientalis) scrublands (pseudomaquis) or woodlands of Quercus coccifera, Carpinus orientalis, Ostrya carpinifolia, etc. occur, while in the higher part (Quercion conferrae) there are forests of mainly deciduous Quercus spp. Extended Pinus nigra forests spread between Querceta-
lia pubescentis and Fagetalia zones. The Fagetalia zone covers the higher parts of the Pindos mountain range, where forests of Abies borisii-regis and mostly of Fagus sylvatica grow. In certain high-altitude parts of the Epirus mountains there are Pinus heldreichii woodlands, which belong to the Vaccinio-Picetalia zone (Pinion heldreichii). Finally, the subalpine vegetation of the Astragalo-Acantholimonetalia zone at the mountain peaks comprises dwarf shrubs, e.g. Juniperus communis subsp. nana, and mainly grasses.

In many cases, the present vegetation has altered to such a degree that its past state cannot be inferred by its current appearance, as a result of the human presence and activity in this region throughout the centuries. According to Bailey (1997), humans have continually inhabited Epirus for 250 000 years and its natural environment has undergone the most intense changes as compared to any other part of Europe.

Information on the vegetation history of an area is provided potentially by palynological research and application of pollen analysis. In the present study an attempt has been made to represent synoptically the temporal vegetation development of Epirus on the basis of data obtained from pollen analysis at various sites of the area.

**Methodology**

Pollen diagrams present concisely the results from applications of pollen analysis and reproduce under certain conditions the successive stages of vegetation in an area. The study and interpretation of a pollen diagram allow not only a reconstruction of the vegetation history, but also provides characteristic information for conclusion-drawing on the factors that affect vegetation and its development (Faegri & Iversen 1989). Absolute dating of a pollen diagram can be achieved with the help of the radiocarbon (C14) dating method.

In every pollen diagram the depicted vegetation development derives not only from the core-sampling area but also, more or less, from a wider region, depending on the 'openness' of the coring site, the existing geomorphological and climatic conditions, and the differential pollen production, dissemination and preservation (Prentice 1985; Spieksma & al. 1994; Sugita 1994). Obviously, data on vegetation development in a closer region to the coring site are more detailed and reliable.

**Human activity in pollen diagrams**

Human activity in the pollen diagrams is principally indicated by plants regarded as anthropogenic indicators and by the ratio of arboreal pollen to non-arboreal pollen (AP: NAP).

Anthropogenic indicators include pollen types directly or indirectly associated with human activity, such as pollen of cultivated plants, weeds and plants associated with grazing, overgrazing, as well as human activities for pasture creation (e.g. Cerealia, Olea, Vitis, Humulus/Cannabis, Rumex, Plantago lanceolata, Asphodelus). Other indicators are the plants characteristic of the destructive human impact on natural vegetation caused by fires, clear-cutting, etc. (e.g., Artemisia, Chenopodiaceae, Juniperus, Pteridium, Poterium/Sanguisorba minor), and species introduced through human activity (e.g. Juglans, Castanea) (Behre 1981, 1990; Bottema 1982; Bottema & Woldring 1990).

A decrease in the AP:NAP values reflects shrinking of the forest cover and, when associated with anthropogenic indicators, could be attributed to human activity. Conversely, an increase in the ratio usually indicates forest expansion, following either the lessening or ceasing of intense human interference in forest vegetation.

**Palynological data from Epirus**

In Epirus, the hydrologic conditions have formed sediments suitable for coring, mainly at low and middle altitudes. Currently, data was attained from a series of pollen diagrams from various sites in Epirus (Fig. 1), in order to present concisely the vegetation history of the area. Most of these diagrams cover a larger or smaller part of the Pleistocene. In fact, diagram É-249 (Tzedakis 1994) covers a period of 423 000 years, which is particularly significant for the vegetation history of the Pleistocene, and not only for Epirus but for a wider region of SE Europe in general. Chronologically, all diagrams extend to the Holocene, but in some of them the later part of that period was not covered, owing to the fact that the corresponding section of the sediment was either missing due to erosion, or did not contain preserved pollen grains. Table 1 shows the palynologically investigated sites in Epirus, the altitude, the zonal vegetation to which they belong according to Dafis (1975), their approximate basal age, and the authors. In Table 2 the pollen assemblage zones of the palynologically investigated sites in Epirus, are grouped in correspondence to the main stages of vegetation development.
Dating
The radiocarbon dating in the various pollen diagrams is in years BP. Along with this, data are given in years or time periods BC/AD, according to the curves of Stuiver & al. (1998a,b) so as to present the events in a more familiar time scale. In some cases a general chronological indication (e.g. centuries, millenia) was preferred, so as to associate the described events to particular historical periods.

Results and discussion

Pleistocene
The Pleistocene is characterized by intense climatic changes, since the glacial periods with their prevailing cold–dry climate alternate with the interglacial periods when the climate was warm and humid. In Southern Europe, the glacial–interglacial cycle had rather a dry–humid character than a cold–warm one. As a result, humidity in that area became the critical factor for the growth of plants (Bottema 1974; Willis 1997).

Table 1. The palynologically investigated sites in Epirus.

<table>
<thead>
<tr>
<th>Site</th>
<th>Altitude (m a.s.l.)</th>
<th>Zonal vegetation</th>
<th>Approximate basal age (years BP)</th>
<th>Authors</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kalodiki</td>
<td>107</td>
<td>Quercetalia ilicis (Quercion ilicis)</td>
<td>24000</td>
<td>Ioakim &amp; Christianis 1997</td>
</tr>
<tr>
<td>Ziros</td>
<td>50</td>
<td></td>
<td>16000</td>
<td>Turner &amp; Sánchez-Goñi 1997</td>
</tr>
<tr>
<td>Gramousti</td>
<td>285</td>
<td>Quercetalia pubescentis (Ostryo-Carpinion orientalis)</td>
<td>14000</td>
<td>Willis 1992a</td>
</tr>
<tr>
<td>Tseravinas</td>
<td>450</td>
<td></td>
<td>16000</td>
<td>Turner &amp; Sánchez-Goñi 1997</td>
</tr>
<tr>
<td>Ioannina I, II</td>
<td>500</td>
<td></td>
<td>&gt; 46000</td>
<td>Bottema 1974</td>
</tr>
<tr>
<td>Ioannina, I - 284</td>
<td>500</td>
<td>Vaccinio-Piceetalia (Pinion – heldreichii)</td>
<td>25000</td>
<td>Lawson &amp; al. 2004</td>
</tr>
<tr>
<td>Ioannina, I - 249</td>
<td>500</td>
<td></td>
<td>243000</td>
<td>Tzedakis 1994</td>
</tr>
<tr>
<td>Rezina</td>
<td>1800</td>
<td></td>
<td>10000</td>
<td>Willis 1992b</td>
</tr>
</tbody>
</table>

Table 2. Grouping of pollen assemblage zones of the palynologically investigated sites in Epirus in correspondence to the main stages of vegetation development.

<table>
<thead>
<tr>
<th>Site</th>
<th>Late Holocene</th>
<th>Early Holocene</th>
<th>Late glacial / Holocene</th>
<th>Late Glacial</th>
<th>Last Glacial (Würm)</th>
<th>Last Interglacial (Eem)</th>
<th>Earlier</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ziros</td>
<td>Z6</td>
<td>Z4</td>
<td>Z3</td>
<td>Z2</td>
<td>Z1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gramousti</td>
<td>GL5, GL6</td>
<td>GL4</td>
<td>GL3</td>
<td>GL1, GL2</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rezina</td>
<td>RM5 to RM8</td>
<td>RM4</td>
<td>RM2, RM3</td>
<td>RM1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tseravinas</td>
<td>TS 5</td>
<td>TS 4</td>
<td>TS 3</td>
<td>TS 2</td>
<td>TS 1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kalodiki</td>
<td>E3</td>
<td>E2</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>E1</td>
</tr>
<tr>
<td>Ioannina I</td>
<td>Y, Z</td>
<td>X</td>
<td>W / X</td>
<td>W</td>
<td>R to V</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ioannina II</td>
<td>Y, Z</td>
<td>X</td>
<td>W / X</td>
<td>W</td>
<td>R to V</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ioannina, I - 284</td>
<td>1-284-1 to 1-284-4</td>
<td>1-284-5 to 1-284-7</td>
<td>1-284-8 - 1-284-10</td>
<td>1-284-11,12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ioannina, I - 249</td>
<td>IN-42 - IN-44</td>
<td>IN-33 - IN-41</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>IN-29 - IN-32</td>
</tr>
</tbody>
</table>
The gradual changes in vegetation during the succession of glacial and interglacial periods can be paralleled to those in Northern Europe, with the significant difference that in Epirus, and more generally in Southern Europe, the various woody species “hibernated” in local refugia during the harsh periods, whereas the corresponding species in Northern Europe had to migrate to areas where they could survive (Bennett & al. 1991).

Glacial periods

According to the data of the pollen diagrams of Epirus, during the glacial periods open steppe vegetation generally prevailed, the dominant species being Artemisia, Chenopodiaceae, Gramineae and Asteraceae. The arboreal species were firmly present although generally with a limited appearance in the vegetation, especially in the lowlands where humidity was lower (Turner & Sánchez-Goñi 1997; Willis 1992a, b, c). However, in Epirus the available moisture even during glacial periods was higher than in the eastern regions of Greece (Tenaghi Philippou), where no arboreal taxa were recorded at the same time (Tzedakis 1994). In the mountainous regions, among certain microenvironments that developed due to the intense geomorphologic conditions, some were characterized by increased humidity and generally favourable conditions for the survival of the forest species, which withdrew there (Willis 1994a).

During the glacial periods, the mountainous regions of Epirus were areas where many species of today’s temperate zone had found shelter and were able to survive for two main reasons. Firstly, the continuous mountain range of the Alps, which begins in Central Europe and runs all the way through to the Pindos Mountains, facilitated the migration of plants between the more northern parts of Europe and the southwest region of Epirus. Secondly, the fact that the cold north winds were blocked due to geomorphology, and especially the highly humid conditions of the Epirus mountain ranges established by the rain-bearing winds from the Ionian Sea, had favoured the appearance of microenvironments suitable for plant survival (Bottema 1974; Willis 1997; Lawson & al. 2004).

The pollen diagrams show very low or minimum values for forest trees (Quercus, Abies, Pinus, etc.) during the glacial periods, which reflect their very limited but nonetheless firm presence in the landscapes of open vegetation (Tzedakis 1993, 1994). Furthermore, during the Late Glacial, in the mountainous region of Rezina the trees that were preserved corresponded to at least ten taxa (Willis 1992b, 1994b). However, as previously mentioned, most species had a very limited presence. Quercus and Pinus prevailed during the glacial phases. Additionally, Abies, which evidently grew in mountainous regions too, had a significant presence; while in cases such as the final stage of the Riss Glacial Period, fir forests were dominant in the wider basin of Ioannina (Bottema 1974). Mention deserves the fact that in order to survive, the ‘European’ fir (Abies alba) withdrew to the Balkan Peninsula and in particular to inland Greece. After hybridisation with the Greek fir (Abies cephalonica) during the last glacial period, the species Abies borisii-regis developed, now dominating the mountain range of Pindos (Athanasiadis 1986).

Interglacial periods

During interglacial periods the vegetation was altering radically and forest vegetation prevailed. It consisted mainly of deciduous broadleaves appearing as mixed oak forests, where the dominant Quercus was accompanied by Ulmus, Tilia, Fraxinus, and Corylus, etc., while the mountainous vegetation was complemented by Fagus, Pinus and Abies. Along with this, the presence of certain species, such as Pistacia and Philyrea, indicated that Mediterranean plant communities developed in certain localities (Turner & Sánchez-Goñi 1997). According to Tzedakis (1994), a distinct forest succession occurred progressively, which “began with expansion of Quercus and Ulmus/Zelkova, followed by Carpinus and to a lesser extent Ostrya, and finally Abies populations increased, often accompanied by Fagus”.

The diagram Ioannina II (Bottema 1974) provides significant data about the last interglacial (Eem). The onset of this stage saw a rapid reduction in fir, while there was an increase in deciduous broadleaved mixed oak forests consisting of Quercus, Ulmus, Tilia, Carpinus betulus, Fraxinus excelsior, Carpinus orientalis, and/or Ostrya carpinifolia, Alnus, Celtis, Buxus, and Parrotia. The appearance of the last three and the increased presence of Buxus (up to 10%) and Parrotia (up to 11%) indicate that during that particular phase, as well as the last interglacial in general, the dominant vegetation at low and intermediate altitudes was different from what it was in the Holocene. By comparing the pollen diagram data, Bottema (1974) argued
on the similarities between the vegetation of the last interglacial to that existing today in the Hycranian forests in Northern Iran. These forests are referred to the class Zelkova-Parrotietea and several of their elements such as Zelkova, Albizia, Gleditsia, Diospyros, etc. are considered to have participated in the composition of the interglacial forest vegetation in Epirus. In addition, Bottema (1974) pointed out that, given the fact that Buxus is generally under-represented in the pollen diagrams, its relatively high percentage values at this particular stage could be explained only by the intensive presence of another tree species, rather than it being the shrub Buxus sempervirens. The occurrence of arboreal species during the last interglacial, which disappeared during the subsequent glacial, is supported by the presence of Parrotia. Along with this, it is evident that climatic conditions during the last glacial were particularly harsh, since some species that had managed to survive during the previous glacial periods had disappeared that time. Finally, considering the current climatic conditions in the Hycranian forests, it appears that during the last interglacial in Epirus, precipitation was higher and the dry period was shorter than it is today.

Late Glacial / Holocene transition

The last glacial (Würm) was characterized by the harshest conditions for plants. While it lasted, a fair number of species, which managed to survive during the preceding glacial periods of the Pleistocene, actually disappeared. More specifically, during the last glacial maximum climate dryness increased a fact which was reflected in the changes of floral composition of the steppe vegetation. Namely, there was an increase in the presence of Artemisia and Chenopodiaceae, while at the same time Asteraceae and Fillipendula had decreased (Turner & Sánchez-Goñi 1997). Towards the end of the Pleistocene and prior to the improvement in the climatic conditions, an increased presence of more thermophilous-hygrophilous forest species was observed. The spread of Quercus at the expense of Pinus and Artemisia, and of Chenopodiaceae at the expense of Gramineae points to a temperature increment. The spread of the thermophilous species, however, shows that the improvement in climatic conditions was of limited duration (Lawson & al. 2004). That stage was paralleled to the corresponding Allerød stage in Northern Europe. The end of the glacial period was characterized by a new deterioration in conditions, a short stage paralleled to the Younger Dryas period in Northern Europe. During that period there was a temporary spread in steppe vegetation as well as a simultaneous increase in the presence of pine and decrease in oak.

The vegetation evidence for the Late Glacial/Holocene transition varies highly between the Greek sites and suggests that response of the vegetation to the Late Glacial climatic changes in Greece was localized (Willis 1992c). According to Willis (1997), the Late Glacial/Holocene transition had occurred in both sites of Gramusti and Rezina around 9800–9300 BP (9270–8600 BC). That time interval could be considered valid for the entire region of Epirus. During that transition a rapid spread of forest vegetation that replaced the steppe vegetation was observed. Almost pure oak forests grew at the low-altitude sites (Ziros, Kalodoki), whereas in the intermediate and higher altitudes (Tseravinas) the broadleaved forests were mixed, with Quercus as dominant species, but also with the presence of Ulmus, Tilia, Fraxinus, Corylus, etc. (Turner & Sánchez-Goñi 1997, Ioakim & Christianis 1997). At the highest sites (Rezina) there was also an intense presence of conifer forests, with prevalence of pine (Willis 1992b).

Generally, in the mountainous regions there was a diversity of forest trees and the various tree species that survived throughout that transitional period gradually spread, as shown by the difference in the AP:NAP ratio between the middle (1:1) and high (3:1) altitudes (Willis 1997).

Holocene

After the onset of the Holocene, the climate continuously warmed up, thus accelerating the spread of forest vegetation over steppe vegetation. Throughout the first millennia, the development and growth of the vegetation was determined almost exclusively by abiotic factors, especially the climate. The first indications of human interference in the natural vegetation appeared in the 6th millennium BC (Turner & Sánchez-Goñi 1997). Subsequently, the anthropogenic impact on the natural environment had become ever more intense and consequently humans played a major role in shaping out the vegetation. The indications of anthropogenic impact on the vegetation had set the criterion for dividing the Holocene into two phases: Early and Late (Willis 1997, Lawson & al. 2004). However, these indications did not appear at
the same time in all pollen diagrams, and therefore the determination of the temporal transition from Early to Late Holocene was based on a rough estimate. Generally for Epirus, it was estimated that transition occurred around the mid 6th millennium BC (5550 BC), considering the age (6635 BP) provided by Turner & Sánchez-Goñi (1997).

Early Holocene (8600–5500 BC)

At low and intermediate altitudes mixed oak forests dominated, which gradually gained larger density, as the diversity of broadleaved woody species increased. Except Quercus, which dominated at first but then showed a gradual decrease, other species of significant presence were Ulmus, Tilia, Fraxinus, Acer, Carpinus orientalis and/or Ostrya carpinifolia, Corylus, etc. During the first millennia of the Holocene, the maximum values of Pistacia pollen, in conjunction with the abundance of Gramineae and the presence of Sanguisorba minor indicated that the mixed deciduous oak forests were fairly open, facilitating the growth of these species. Pistacia terebinthus must have been the dominant species during that period, since the absence of macquis vegetation elements indicated that the climatic conditions, besides being relatively dry, were too cold to allow the growth of Pistacia lentiscus (Bottema 1974; Lawson & al. 2004). The subsequent withdrawal of Pistacia and Sanguisorba minor and the expansion of broadleaved trees could be attributed to a change in the climatic conditions and in particular to an increase in precipitation.

During the first millennia of the Holocene, ca 8600 to 6400 BC (9300–7500 BP), dense mixed oak forests dominated the mountainous regions of Epirus, increasing the AP:NAAP ratio to 10:1 as shown in the Rezina diagram (Willis 1992b, 1997). By the mid 7th millennium BC (7500 BP), fir showed a significant increase and became the main component of forest vegetation (Willis 1992b, c). That fact, along with the presence of other species, such as Fagus, Carpinus betulus, etc., was also related to the climatic changes mentioned above.

Late Holocene (5500 BC – Present)

In spite of the fact that the development of vegetation was largely determined by the impact of abiotic factors, especially the climate, during the first millennia of that period (5500–2000 BC) human presence and interference in vegetation was ever more frequently traced out in the pollen diagrams. In fact, there were specific cases where the actual results of that interference determined the development of vegetation. As a rule, however, these events tended to have a local effect. As from the mid 3rd millennium BC and thereafter, human impact on the vegetation of Epirus and generally across Greece had not only gradually intensified but occurred on a larger scale (Gerasimidis 1995). Moreover, anthropogenic disturbance in the majority of cases formed in the Balkan regions the present-day landscape during the three millennia BC (between 4500 and 2000 BP) (Willis 1994a).

Around the mid 6th millennium BC (6635 BP), there appeared to have been a significant decrease in Quercus, along with forest vegetation in general, as shown in the Tseravinas diagram. The simultaneous increase of certain herbs, such as Artemisia, Plantago and in particular of Pteridium, was associated with intense grazing activity in the area. In the corresponding sediment section, the abundance of charcoal indicated that the vegetation in the area was extensively burnt out, most likely for creation of pastures. This is the earliest indication of an anthropogenic impact on the natural environment in Greece and generally in the Balkans. Open vegetation continued to mark the landscape and around 2500 BC (about 4000 BP) became ever more pronounced (Turner & Sánchez-Goñi 1997).

The Gramoustis diagram shows similar events (Willis 1992a, c). Already since the end of the 5th millennium BC (5200 BP) there was a significant decrease in all woody species and a substantial increase in herbaceous vegetation. The severe limitation of forest vegetation caused erosion and soil degradation, as indicated by the influx of allochthonous material in the sediment accumulated during that phase, as well as the increase in Compositae. Deterioration of soil conditions was partly irreversible. That can be seen in the following phase from ca 3800 to 2500 BC (from ca 5000 to 4000 BP), when despite the large re-expansion of woodland vegetation (AP:NAP=7:1), species diversity was quite limited. Moreover, it is likely that part of the AP values originated from kermes oak scrub, which developed as a result of grazing*. During the last millennia, vegetation resembling pseudomacquis

* In the Gramoustis and Rezina diagrams no distinction was made between evergreen and deciduous oaks, according to the two types of pollen – Quercus ilex-type and Quercus robur-type – which include the pollen of the evergreen and deciduous oaks respectively.
remained relatively stable, with *Quercus* (possibly *Q. coccifera*), *Carpinus orientalis* and/or *Ostrya carpinifolia* as dominant species (Willis 1997).

The decisive role of human impact on the development of vegetation can be traced clearly out in the diagrams of the region of Ioannina. Their data do not coincide chronologically with those of Tseravina and Gramousti diagrams, thus making difficult any generalizations about the temporal vegetation development in Epirus. Nevertheless, the vegetation in the various regions appeared to have evolved differently as a result of early human activity, which was manifested differently from area to area.

In Ioannina, forest vegetation decreased during the period 4500–2400 BC (5700–3900 BP), while the taxa associated with animal husbandry and agriculture increased (Lawson & al. 2004). Since 2400 BC (3900 BP) and until 250 BC (2220 BP), however, the area seemed to have experienced an exceptional re-expansion of woodland vegetation, considering the extreme soil erosion that occurred previously. While mixed deciduous forests of similar composition with those of the Early Holocene had developed, the conifers, and especially *Abies*, did not fully recover, perhaps due to the fact that the ecosystems at high altitudes were more susceptible to soil erosion. Along with this, there was an increase in the ratio of evergreen/deciduous oaks, most probably as a result of grazing pressure, while the abundance of cereals indicated intensification of the agricultural activity in the Ioannina basin. The traced out agricultural and pastoral activity was puzzling, considering the observable re-establishment of the forest. Most likely, anthropogenic activity was limited to low altitudes. The transfer of these activities to the mountainous regions appeared often in the pollen diagrams of Greece and was associated with the appearance or spread of *Carpinus orientalis* and/or *Ostrya carpinifolia*, as well as of such evergreen broadleaves as *Quercus coccifera* and/or *Q. ilex*, *Phillyrea* and *Olea*. The latter, in combination with *Pistacia, Spartium* and *Cistus* indicated the development of Mediterranean vegetation (maquis) similar to the present-day vegetation in the region at altitudes up to about 400 m.

A further decline in oak woodlands and a subsequent increase in the indicators of open vegetation (*Taraxacum*-type and *Centaurea*-type) were associated with the increase of cultivated plants plants, which were mainly cereals and to a lesser extent vineyards, olives and walnut trees (Turner & Sánchez-Goñi 1997).

With the onset of the Late Holocene, forest vegetation began to withdraw in the mountainous regions, resulting in a AP:NAP value of 2:1. The shrinking of forests could be attributed exclusively to sustained soil erosion because of increased precipitation, but mainly to anthropogenic destruction of the forest vegetation, considering the indication of anthropogenic interference in the vegetation of the lower regions, as well as the increased input of allochthonous material in the sediments accumulated during that period (Willis 1997). That hypothesis was supported by the simultaneous increase of the herbaceous species diversity, a feature which marks the beginning of the anthropogenic interference in an area (Birks 1986). The absence of cultivation indicators points to clear-cuttings for the purposes of animal husbandry rather than agriculture. In fact, the modern clearing of low and high areas supports the hypothesis of seasonal movement of herds also in the past; i.e. in winter the livestock was kept in the lowlands and in summer it was moved to the mountainous pastures (Willis 1997).

Around 2500 BC (ca. 4000 BP), another deforestation made the AP:NAP ratio decrease further to 1:1, a value corresponding to the last glacial phase. The shrinking of mountainous forest vegetation in conjunction with intense grazing caused strong soil
erosion and created conditions for the development of herbaceous vegetation consisting of such taxa as Chenopodiaceae, Artemisia, Rumex, etc. The Rezina diagram indicates that the downward movement of the tree line, the degradation of forest vegetation, and the final shaping out of vegetation to its present state had started already about 2000 BC. (Willis 1992b).

Despite all this, the development of pine forests in the period between ca 0-800 AD (ca 1990–1200 BP) showed that preconditions still existed for the growth of forests, which, however, lacked the diversity of the mixed forests of the first millennia of the Holocene. The expansion of pine forests was attributed to either a rise in precipitation or to a decline in human activity in the mountainous regions during that period (or even perhaps to combination of the two). However, since the beginning of the last millennium, open grasslands caused by grazing pressure have been the dominant elements in the vegetation of the mountainous regions until now. Willis (1997) pointed out that current vegetation is in conflict with what it was in the past, prior to human impact. The result was that the mountainous regions were deforested, while oak forests grew abundantly in the lowlands, even though they consisted mainly of kermes oak scrub, which have replaced the grazing-degraded mixed deciduous oak forests.

Conclusions

According to the palynological data, the general conclusions about the vegetation history of Epirus are the following:

Pleistocene. During the glacial periods open steppe vegetation generally prevailed. However, arbooreal species were firmly present, although with a generally limited occurrence in the vegetation. In the mountainous regions, certain microenvironments characterized by favourable conditions, were cited as refugia for temperate taxa. During the interglacial periods the vegetation altered radically and forest vegetation prevailed. It consisted mainly of deciduous broadleaves appearing as mixed oak forests, while the mountainous vegetation was complemented by Fagus, Pinus and Abies.

Late Glacial/Holocene transition. A rapid spread of forest vegetation replaced the steppe vegetation. At low altitudes almost pure oak forests grew, while at the intermediate altitudes there were mixed oak forests. At high altitudes conifer forests developed, in which pine prevailed.

Holocene. The Holocene is divided into Early and Late Holocene. This division is based on the first palynological data on the anthropogenic impact on the vegetation, which for Epirus dates back to about the mid 6th millennium BC: the earliest data in Greece and generally in the Balkans.

Early Holocene. Throughout that period, the development and growth of the vegetation was determined almost exclusively by abiotic factors, especially the climate. At low and intermediate altitudes pure oak forests gradually gained larger density and diversity and expanded to higher places. At high altitudes, in the beech and coniferous forests, fir became the main component of the forest vegetation.

Late Holocene. That last period was characterized by the anthropogenic impact on natural vegetation. The first indications of these events in Epirus appeared in the mid 6th millennium BC. Subsequently, anthropogenic disturbance of the natural environment became ever more intense and consequently humans played a major role in shaping out the vegetation. The most important changes in natural vegetation were degradation of the mixed oak forests at low and medium altitudes into macquis and pseudomaquis, as well as formation and gradual downward movement of the mountain treeline at the highest altitudes.

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References


