A new framework for understanding Pannonian vegetation patterns: regularities, deviations and uniqueness

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Abstract: In this paper, we elaborated a new concept (the Regularities-Deviations-Uniqueness; RDU framework) to analyse regional vegetation patterns and applied it to the Pannonian region of the Carpathian Basin. We introduced three criteria, namely: distributional regularity, distributional deviation, and compositional uniqueness. Regularities conform to the pattern expected based on macroclimate and relief. Deviations are singular phenomena and are defined as the conspicuous departures from the regular pattern at odds with either zonal pattern (climate rules), or the repetitive extrazonal patterns (relief and meso-climate interactions). Endemic plant communities of the Pannonian region (defined by a unique species composition) are regarded as the unique features. The main regularities recognised for the Pannonian region are: (1) the altitudinal pattern of vegetation belts, (2) the horizontal zonation of the Dunántúl, (3) the gradient of continentality along the mountain ranges, and (4) the circular zonality of the Nagyalföld. Deviations are mostly explained by local vegetation history, mesoclimate, and edaphic factors. The major deviations include (i) occurrence of mixed *Pinus sylvestris* forests in Őrség, (ii) cool continental forest–steppe forests on Kisalföld, and Gödöllői-dombvidék, (iii) the direct contact of *Fagus* and *Quercus pubescens* forests (Bakony, Balatonfelvidék), (iv) the *Fraxinus excelsior–Tilia* spp. forests on rock outcrops, and (v) the *Sphagnum* bogs on the Alföld. Individuality of the Pannonian region is demonstrated by the endemic zonal forest–steppe forests and intrazonal endemic communities such as the *Cerasus mahaleb–Quercus pubescens* forests, and the vegetation on calcareous sand, dolomite and saline soils and the like. We argue that the introduced criteria are suitable for the entitation and description of other biogeographical regions, and offer useful tool for interregional comparisons.

Nomenclature: Vascular plant names follow Euro+Med (2006-2013).

In memory of Bálint Zólyomi

1 Introduction

The flora and vegetation of the Pannonian region in the Carpathian Basin, which is situated southeast in the heart of Central Europe, is unique in several aspects. Resulting from its location it is a crossroads for the European, sub-mediterranean and eastern-continental species and vegetation types (see Pócs 2000). The continental European latitudinal system of zonobiomes becomes distorted in this basin due to the constellation of the surrounding mountain chains (Varga 1989, 1995). These made the Pannonian region of interest for the analysis of large-scale vegetation patterns that is also supported by the considerable amount of literature and accumulated expert knowledge waiting for a synthesis.

The landscape and region as spatial scales of vegetation phenomena

In our paper we focus on landscape and coarser scale patterns and phenomena. There is a variety of landscape definitions (e.g., Forman and Gordon 1986, Zonneveld 1990,

Gergel and Turner 2002, Élesztős and Rostás 2003). We take the holistic approach and define landscape as a uniform part of the Earth surface that is a result of interactions between geological, climatic and ecological factors and that is distinct from other land-units in terms of geology, topography, hydrology, and biota (Kádár 1965, 1975, Kondracki 1966, Zonneveld 1990, Élesztős and Rostás 2003).

Plant communities in a landscape interact with one another at the centuries time scales through species pools, cycles of nutrients, water, creating unique vegetation-landscape patterns reflecting historical assembly modified (in the last centuries in particular) by human influences. Nonetheless, besides differences that make neighbouring landscapes distinct (enhanced when barriers between landscapes are strong), landscapes also share features that allow their classification into larger-scale units (e.g., Küchler 1973, Bailey 1996, Leser et al. 1997). If vegetation is of main concern, the region can be viewed as an area composed of several landscapes that are geographically more or less homogeneous and have similar vegetation or similar repeated mosaics of different landscapes. The variability of the species composition of plant communities, their position in the vegetation complex, and the regularities of their spatial distribution may be best as-

sessed by studying the repetitions within the landscapes of a region. Even the range of 'endemic' communities usually encompasses several landscapes. Thus, it is not only the landscape scale, but also the region that may represent a natural scale in the spatial division of the vegetation (Dierschke 1994). Biogeography also acknowledges this as demonstrated by the considerable literature on the delineation of biogeographical regions (Brown and Lomolino 1998, Cox 2001, Rueda et al. 2006 etc.).

Vegetation science uses many tools to recognize and describe vegetation patterns. Among those the use of species composition to recognize and characterize vegetation (such as associations), and mapping (spatial presentation and analysis) of the recognised vegetation units are the most widely ones used in Central Europe, dominated by the Braun-Blanquet approach (Braun-Blanquet 1964; Westhoff and van der Maarel 1973, Dierschke 1994) and known also the as Zürich-Montpellier method. Importantly, this approach also recognises the vegetation geographical aspect addressing for instance the determination of distribution ranges of the vegetation units and their role in landscapes and larger geographic framework. The practicing of so called 'synchorology' (Dierschke 1994) as part of phytosociology has lead to the recognition of endemic associations (for seminal papers on the topic pertinent to Hungary by Rezső Soó (Soó 1964, 1968, 1973, 1980, and literatures cited therein) and by Attila Borhidi (Borhidi 2003, Borhidi et al. 2013). The role of vegetation mapping (seen by phytosociologists as part of 'synchorology') typically produces vegetation maps – spatial models of vegetation for landscapes or for smaller localities (for an overview of Hungarian vegetation maps consult Fekete 1999); country-scale maps pertinent to our region have also been constructed (e.g., Zólyomi 1967, 1989, Niklfeld 1973, Michalko et al. 1986).

A new approach to analysis of vegetation pattern at broader scales

Here we introduce an approach, long time in making and with elements appearing in the literature earlier (Fekete and Varga 2006, Fekete et al. 2012). We suggest that the following three criteria are of vital importance to understand the vegetation patterns at regional scale: distributional regularity, distributional deviation and compositional uniqueness.

1. *Distributional regularity.* On a vegetation map, a whole series of spatial arrangement patterns may be seen. It is the spatial order of plant communities on the maps as well as their spatial position relative to others that are more or less consistently repeated in space. The series of arrangements eventually leads to the recognition of regularities of distribution (or shortly *regularity*) that determine the structure of the vegetation mosaic. Such regularities often may be identified on coarse-scale potential-vegetation (Tüxen 1956) maps depicting usually zonal vegetation phenomena. In fact, these regularities make prediction possible and contribute to the definition of regional rules.

2. *Distributional deviation.* The rules, which manifest themselves in spatial regularities, may occasionally be violated. In order to cover this case, we introduce a second criterion –distributional deviation or shortly *deviation* that we define as a conspicuous departure of the studied vegetation phenomenon from the expected pattern (expected either by expert knowledge or by modelling predictions based on macroclimate alone). Deviation is a unique phenomenon. Patterns that occur repeatedly are not considered as deviations. To our knowledge the term 'deviation' has not been used in vegetation-ecological literature in this connotation so far.

Regularities and deviations also develop at fine scales. Here, vegetation units exhibit rather clear preferences regarding abiotic factors (for Hungarian examples, see Bölöni et al. 2011). Deviations occur where prediction of vegetation units is uncertain if abiotic variables are used as explanatory variables and thus the observed vegetation is different from the predicted. Such patterns may arise due to the stochasticity of vegetation–environment relationships, which is also apparent from predictive vegetation models (e.g., Davis and Goetz 1990, Brzeziecki et al. 1993, Franklin 1995, Aszalós and Horváth 1998).

3. *Compositional uniqueness.* Endemic plant communities exhibit unique species composition (compositional uniqueness or shortly 'uniqueness'). These syntaxa do not occur in any other regions (or if they do, their presence is insignificant or very localised). The identity/uniqueness of a region when defined by the vegetation is primarily based on its endemic communities.

For the sake of brevity, we suggest to call our approach, based on three corner-stone concepts as the RDU (Regularity-Deviation-Uniqueness) conceptual framework.

2 Regularities

In our paper, we present a novel and succinct discussion of the Pannonian vegetation on the basis of the three corner stones of our new conceptual framework. This paper is an advanced version of the previous paper published in Hungarian (Fekete et al. 2012).

As one of the most complete basins of the Earth, the Carpathian Basin does not favour the development of wide zones and belts with zonal vegetation (Varga 1989, 1995, Zólyomi 1989) (Table 1).

2.1 Vegetation belts

The main coarse-scale regularity in the Pannonian region is the spatial pattern of vegetation belts in the mountains, especially in the higher mountains of the Északi-középhegység (see Fig. 1, for the Hungarian toponymy). In most parts of the region, the altitudinally lowest belt is the forest–steppe belt in the Alföld. This belt tapers out at ca. 220–230 m of altitude on the foothills, and it is followed usually by *Quercus cerris–Q. petraea* forests or occasionally (due to mesoclimatic reasons) by *Q. pubescens* forests. The next belt is the *Quercus petraea–Carpinus betulus* forest belt, followed by the sub-

Table 1. Vegetation pattern regularities of the Pannonian region.

Phenomenon	Landscape
Spatial pattern of vegetation belts: altitudinal gradient of communities (from forest steppe at low altitudes to beech forests at high altitudes) with a shift of vegetation belts upwards in the mountains with continental climate	Magyar-középhegység
Spatial pattern of vegetation zones: horizontal gradient of communities from east to west (from forest-steppe to beech forests)	Dunántúl
Gradual disappearance of sub-mediterranean communities widespread in the Dunántúli-középhegység towards north-east, and of communities with continental character widespread in the Északi-középhegység towards south-west	Magyar-középhegység
Circular vegetation pattern of the Nagyalföld	Nagyalföld

Figure 1. The map of the study region with the Hungarian toponymy used in the paper.

montane *Fagus sylvatica* forests, and in the highest mountain ranges of the region – the montane beech forests.

2.2 Zonal pattern in the Dunántúl

Another observed regularity is the west–east zonal pattern observed in the Dunántúl. The altitudinal belts of the forest types typical for the Pannonian mountains develop here at similar altitudes adjacent to one another, from the sub-atlantic and sub-mediterranean western Dunántúl to the more continental eastern Dunántúl as follows: beech forests, oak–hornbeam forests, sessile oak–turkey oak forests and partly pubescent oak forests, and the open forests of the forest steppe. The similarity of the patterns of altitudinal belts and latitudinal zones may be attributed to a basin effect, i.e., the strong continental influence of the Nagyalföld on the one hand, and the effect of the surrounding high mountains on the other.

Quercus cerris–Q. petraea forests have been the most extensive forests in Hungary since ca. 8000 cal BP. This com-

munity is typical of both types of zonal patterns (latitudinal zones and altitudinal belts). These forests prefer deep soils, and therefore the majority of them occurs on level terrain or on gentle slopes. They may form a belt of substantial size – as wide as 400 meters. The growth of the two oak species is suboptimal in this environment, so they may survive at both margins of the belt, while their proportion changes accordingly. The lower boundary of their belt is at altitudes spanning 230–250 m in the mountains. The upper boundary is often at about 500 m, but this value is quite variable. In the Északi-középhegység, they reach altitudes as high as 600–650 m, and exceptionally up to 800 m (Kovács 1975). Increasing continentality towards the northeast is supposed to drive these patterns. The forest–steppe belt also ends at higher altitudes at these places. In the Mátra Mts, for example, forest–steppes may occur at exceptionally high altitudes, such as 300–350 m just below the belt of the closed *Quercus petraea–Quercus cerris* forests.

Table 2. Vegetation deviation phenomena in the Pannonian region.

Phenomenon	Landscape	Putative cause of appearance or survival
Mixed deciduous-coniferous forests	Western Dunántúl (Őrség)	Vegetation history; mesoclimatic (sub-Atlantic climate) and edaphic factors (acid gravels)
Pinus sylvestris forests of cool-continental forest steppe	Kisalföld	Vegetation history; local climatic and edaphic factors (sand)
Deciduous forests of cool-continental forest steppe	Gödöllői-dombvidék	Mesoclimatic and edaphic factors to a smaller extent
Illyrian type distribution of vegetation belts	Bakony, Balatonfelvidék	Early postglacial appearance of *Fagus sylvatica*; climate-induced decrease in the vitality of subcontinental forests
Mixed *Tilia –Fraxinus excelsior* forests	Északi-középhegység	Early postglacial appearance of *Tilia* and *Fraxinus* before *Fagus;* competitive superiority of *Tilia* to *Fagus* in specific rocky outcrop habitat
Raised bogs at low altitudes	northern Alföld, Északi-középhegység	Vegetation history; mesoclimatic factors; Alföld: also edaphic factors (oxbows of meandering rivers on acidic substrate, oligotrophic groundwater)

2.3 Climate gradient along the Magyar-középhegység

Another important regularity in the Pannonian region is the climate gradient along the Magyar-középhegység from southwest to northeast (Zólyomi et al. 1992). Several, mainly sub-mediterranean plant communities (e.g., both open and closed *Quercus pubescens–Fraxinus ornus* forests, dolomite grasslands; Jakucs 1961, Kun et al. 2000) widespread in the southwest (Dunántúli-középhegység) disappear towards northeast (either within this mountain range, or east of the Danube, in the western part of the Északi-középhegység). On the other hand, the frequency of several plant communities of continental character, mainly distributed in the northeast (e.g., various calcareous rocky grasslands, *Spiraea media* scrub), diminishes towards southwest (Zólyomi 1942).

2.4 Circular zonation in the Nagyalföld

As a consequence of the macroclimatic gradients from the periphery of the Nagyalföld towards the center of the basin, closed broadleaved deciduous forests cover the margins of the Nagyalföld in the north, north-east and east, and in the valleys of the Drava and Sava Rivers, while the greatest part of the Nagyalföld belongs to the forest–steppe zone (Fekete et al. 2010). Vegetation of the landscapes of the forest–steppe zone of the Nagyalföld mostly differs due to edaphic factors, primarily geological substrate (loess, calcareous and acid sand, saline soils on loose sand or hard clay; Kádár 1965), and hydrology (azonal aquatic vegetation). Species composition of plant communities on sand, saline soils, and on dry loess is clearly distinct from each other as well as from the zonal plant communities of the Pannonian forest zone. Yet even if the azonal vegetation is edaphically controlled, gradients indicating climatic control may be demonstrated (e.g.,

the strong gradients of forest and steppe species from the periphery of the Alföld towards its center; Fekete et al. 2010).

3 Deviations

Vegetation pattern deviations are exemplified always by individual causes that may not be easily formalised (Table 2). We may distinguish zonal and extrazonal deviations in vegetation patterning. The zonal deviations are conspicuous differences between the actual potential vegetation (*sensu* Somodi et al. 2012; for the closest approximation for Hungary, see Zólyomi 1989) and macroclimate-based expectations (Borhidi 1961). The extrazonal deviations are recognisable on potential vegetation maps, as unexpected individual features.

Extrazonal vegetation (sensu Walter and Breckle 1991) is commonly encountered in the study region. Typically, it can be mapped and predicted well, since its occurrence follows clear rules. Extrazonal stands usually occur close to their zonal occurrences, e.g., either on south- or on north-facing slopes. Extrazonal stands interpreted as deviations, however, are far from their zonal occurrences. The most apparent deviations that are the most suitable for the characterization of a region occur at the landscape level, and therefore we shall discuss them within the context of selected subregions. The last two examples, however, apply to finer scales and thus are discussed in the landscape context.

3.1 Őrség, Western Dunántúl

Perhaps the most apparent example of a deviation at the landscape scale is found in the Western Dunántúl. Here, in several landscapes, but primarily in Őrség, extensive stands of *Pinus sylvestris* intermixed with deciduous trees occur (Pócs

1960, Tímár 2002). It is known that *Pinus sylvestris* was present in Dunántúl during the last glaciation and formed patches of open taiga forest (Rudner and Sümegi 2001). These were transformed into closed and mixed taiga forests during the late glacial period (Willis 1997, Szántó and Medzihradszky 2004, Juhász and Szegvári 2007). Survival of *Pinus* to the early and middle Holocene in Dunántúl is highly probable (Szántó and Medzihradszky 2004). 25–50% proportion of *Pinus* in the majority of pollen diagrams until 6700–7000 cal BP suggest that *Pinus* formed mixed forests with deciduous trees such as *Quercus*, *Corylus*, *Ulmus*, *Fraxinus*, *Fagus* in the Bakony, west of the Lake Balaton and possibly also in the Őrség. Retreat of *Pinus* to nutrient-poor habitats took place very likely during the second half of the Middle Holocene (8200-4200 cal BP; Walker et al. 2012), owing to the expansion of *Quercus*, *Fagus* and *Carpinus betulus*. The frequency of *Pinus* in the early Holocene can likely be explained by climatic factors. Similar forest composition has developed in the broader Baltic region, including Northern Poland, Belarus, and the neighbouring Russia. The boreo–continental, Illyrian and dealpine species of the Pannonian *Pinus* forests in Őrség probably appeared in several waves during the Würm (probably during the first cooling of the würm starting around 110 kyr BP) and the early postglacial periods with cool-continental climate, although direct evidence for this is still missing. Intermingling of these floristic elements rendered the local communities a unique character. By today, the likely direct connection to the Baltic *Pinus sylvestris* forests during the late glacial forest expansion has had diminished. Typical communities in the West-Dunántúl, especially in Őrség, such as transitional mires, willow swamps and fens, *Calluna* heath, birch heath, etc. (see Pócs et al. 1958), are rare in other parts of the Pannonian region. The reason why the presence of mixed *Pinus* forests is interpreted as a deviation is that the transformation of vegetation into pure broadleaved forests, such as acidophilous beech or oak forests did not take place here.

3.2 Kisalföld

Pinus sylvestris disappeared on the Alföld about 9800–10 000 years BP (Magyari et al. 2008, 2010) with one notable exception – the Kisalföld. There, in the vicinity of the cooler Bakony Mts at the border of the Dunántúli-középhegység (at Fenyőfő), pine stands grow on calcareous windblown sands. Beneath the loose forest canopy, the herbaceous vegetation receives enough light, and therefore plants typical of sandy grasslands co-occur here alongside few species typical of the pine forests (*Monotropa hypopitys*, *Pyrola chlorantha*, *Veronica officinalis*, etc.). The cover of mosses typical of coniferous forests is considerable on the forest floor. Some of the *Pinus* stands at Fenyőfő are considered autochthonous; most of them, however, are plantations dating from the 19th and 20th centuries (Pócs 1966, Majer 1988, Kevey 2008).

These forests cannot be regarded as a representative of the sub-mediterranean forest steppe, but rather as those of the northern cool-continental forest-steppe (cf. Niklfeld 1974). They are also similar to forests of the Ukrainian–Russian forest–steppe zone (Didukh et al. 2011). Their presence in the Pannonian region is regarded a deviation. According to pollen analytical studies (Mezőlak near Pápa; Juhász and Szegvári 2007), *Pinus sylvestris* was dominant during the early Holocene up to 6800–7000 cal BP, and was less abundant later (5–20%; Juhász and Szegvári 2007). According to Juhász and Szegvári (2007), the high Early Holocene pollen frequencies suggest the last glacial origin of the *Pinus* forests in the Kisalföld (see also Sümegi 2007).

3.3 Gödöllői-dombvidék

Forests of the East European cool-continental forest–steppe zone are primarily composed of broadleaved deciduous trees rather than of conifers (Niklfeld 1974). Occurrence of such forests in the Carpathian Basin was hardly noticed until the 1960s when Fekete (1965) recorded that the usual altitudinal regularity of forest communities in the Északi-középhegység was disrupted in the Gödöllői-dombvidék. The relatively low hilltops were not covered by the Pannonian *Quercus cerris–Q. petraea* forests as expected. Instead, the zonal forests there are represented by dry oak–hornbeam forests in which *Acer campestre*, a common accompanying species elsewhere, is abundant and grows into the upper canopy layer reaching the height of *Carpinus betulus* and the two local oak species (*Quercus petraea* and *Q. robur*) and their hybrids. Unlike in the widely distributed oak–hornbeam forests in the country, elements of dry oak forests also occur in the herb layer of the *Acer campestre*-rich dry oak–hornbeam forests. The deviation is caused by the mesoclimate of the Gödöllői-dombvidék that appears to be more continental then the areas at the same altitude in the Északi-középhegység since the Gödöllői-dombvidék is almost completely surrounded by the warm lowlands of the Nagyalföld. The mean temperature is slightly lower, however. The role and abundance of the associated tree species (*Fraxinus excelsior, Tilia cordata, Acer* spp.) increase in the deciduous forests towards the east of Europe. In Western Moldavia and partly also in Ukraine, steppe forests, *Quercus robur* and *Fraxinus excelsior* are widespread (Bohn et al. 2000, Didukh et al. 2011). The oak–hornbeam forests with *Acer campestre* in the Gödöllői-dombvidék are in fact representatives of the deciduous forests of the East European cool-continental forest–steppe zone, with very similar species composition as those in Ukraine (Fekete 1965, Gribova et al. 1980, Molnár et al. 2008). Thus, this forest community is a deciduous equivalent of the *Pinus sylvestris* forests of the Kisalföld. The direct spatial connection of the forests of the Gödöllői-dombvidék to the cool-continental forest–steppe forests of Western Ukraine was most probable in earlier phases of the Holocene. Similar forests exist in form of small stands in northern Hungary and as rather extensive forests in the Mezőség (Câmpia Transilvaniei) in Transylvania, Romania. The link to the east is further emphasized by the fact that forest–steppe forests dominated by *Tilia cordata* were also identified in the Gödöllői-dombvidék on sandy soils (Fekete 1965). Such forests are encountered in the eastern part of the Russian forest–steppe zone between the Volga and Ural Rivers in Bashkortostan (Khairetdinov 2004)

and have been recently reported to occur also in the Southern Urals (Chytrý et al. 2010). As shown by pollen diagrams, similar forests with variable associate composition were widely distributed in the Nagyalföld and at the foothills of the Északi-középhegység in the Early Holocene (i.e., *Tilia* dominance at Bátorliget between 11,200 and 10,800 cal BP; Willis et al. 1997, Magyari 2002a). The development of the forest–steppe forest with *Tilia* in the Gödöllői-dombvidék may also have commenced in the Early Holocene (Willis et al. 1997).

3.4 Bakony and Balatonfelvidék

The absence of expected vegetation belts is also a sign of vegetation pattern deviation. This has been observed, for instance, in the Dunántúli-középhegység north of the Lake Balaton (Bakony and Balatonfelvidék). At about 400 m of altitude in the Bakony Mts, plateaus and gentle slopes are covered by beech forests. South of the Veszprém-Nagyvázsony line, towards the Balaton Lake, the potential vegetation patterns change abruptly. The hilltops and plateaus are covered by dry oak scrub forests dominated by *Cotinus coggygria, Quercus pubescens* and *Fraxinus ornus*, while tall-grown beech forests are restricted to the north-facing slopes (Fekete and Zólyomi 1966). Not one, but two vegetation belts are missing here: the sub-continental *Q. cerris–Quercus petraea* and the *Quercus petraea–Carpinus betulus* forests that regularly develop in these positions elsewhere in the Pannonian region. This situation is well documented on the potential vegetation map of Zólyomi (1989), while it is lacking on the map of zonal vegetation by Borhidi (1961) that was modelled on climate data as depicted in Walter-Lieth diagrams available for the mapping area. The close vicinity and even direct contact of the belts of mesic beech forests and dry pubescent oak forests, and their occurrence at the same altitude are unexpected in the Pannonian region. This phenomenon, however, exists elsewhere at a larger scale as for instance in the northern part of the Dalmatian Karst as documented by the vegetation map made by Horvat (1962). A belt of pubescent oak forests is situated adjacent to the montane–submontane beech forests in the southern regions of the Eastern Alps as well as along the Adriatic coast (Bohn et al. 2000). One reason for the lack of vegetation belts in the Bakony–Balatonfelvidék area is a sudden change in climatic conditions. Coming from the north, moist air is forced upward by the Bakony Mts that leads to moisture precipitation in the northern section of the area. This provides humid mesoclimatic conditions for beech forests. In the southern section, on the Balatonfelvidék, descending warm air masses create a rain shadow, which leads to the dominance of dry oak scrub forests.

This unusual spatial pattern of zonal communities could not have emerged if it had not been for the local vegetation history. Pollen and macrofossil data indicate that beech survived in small populations in the territory of Slovenia and on the Istrian Peninsula during the early interstadial stages of the Würm period (Culiberg and Sercelj 1995, Willis and van Andel 2004, Magri et al. 2006). Migration of beech starting from this refuge may be detected during the early stages of the postglacial period between 11,500–10,200 yrs BP re-

sulting in beech abundance increasing rapidly in the Eastern Alps and in Western Hungary (Magyari 2002b, Magri et al. 2006). Beech was detected in the Early Holocene north of the Lake Balaton between 8650 and 7950 cal BP (Juhász 2007). The first maximum pollen density of beech in the Balaton area was detected between 8000 and 6000 cal BP (Magyari 2002b), just at the time when sub-mediterranean oak forests were the most extended (Lang 1994). We conclude that the current vegetation pattern may have developed rather early. At the beginning of this period, the xero-thermophilous character of the oak forests is indicated by the presence of *Cotinus coggygria* (Zólyomi in Fekete and Zólyomi 1966). Besides the early beech dominance, *Ostrya/Carpinus orientalis* was also detected (Fekete and Zólyomi 1966). *Ostrya carpinifolia* is a frequent and dominant species of mixed *Quercus pubescens–Fraxinus ornus–Carpinus orientalis* forests bordering on beech forests at the foothills of the Eastern Alps and in the Illyrian region. The unusual vegetation history of the Bakony-Balatonfelvidék area also explains unique biogeographical phenomena, such as the fairly isolated occurrence of several West-Balkan elements (e.g., *Achnatherum (Stipa) bromoides, Aethionema saxatile, Amelanchier ovalis, Chaerophyllum nodosus, Daphne laureola, Hippocrepis emerus, Prospero elisae,* and *Scutellaria columnae*). This area constitutes one of the hot spots of floristic diversity in the Pannonian region.

3.5 Rocky forests in the Északi-középhegység

Deviation examples 1 through 4 represent deviations at the landscape scale. Deviations, however, are also observable at finer spatial scales. One of the most prominent examples is the case of forests on rocky outcrops and screes. On rocky slopes, periglacial screes of the Magyar-középhegység the high abundance of *Tilia* species is common resulting in forests resembling oak–hornbeam forests apart from the presence of *Tilia* in the canopy. In certain rocky slopes of the Északi-középhegység though, the species composition of forests is different even though the habitat is similar. The stands of these forests are dominated by lime (*Tilia platyphyllos*) and by ash (*Fraxinus excelsior*) and they form isolated islets in the sea of the surrounding zonal oak–hornbeam and beech forests (Zólyomi 1967). The dominant understorey species of this intrazonal community are elements of oak forests that are associated with species showing disjunct distributions, such as *Andraea rupestris, Carex brevicollis, Waldsteinia geoides*, etc. The main shrub component along the forest fringe of these forests is the eurosiberian–continental *Spiraea media,* associated with *Cotoneaster niger*, *Rosa spinosissima*, and many forest–steppe elements. At some locations continental meadow steppes with *Dracocephalum ruyschiana* also enter this vegetation mosaic. This continental mountain vegetation mosaic is separated from the forest–steppe belt of the foothills and lowlands by one or two, several hundred meters broad forest belts. Both ash and lime appeared earlier in the Északi-középhegység than beech. According to pollen data, ash and lime appeared in the mountains in 9600–9500 cal BP, whereas the first occurrence of beech is estimated at 6000 cal BP (Willis et al. 1997). The Holocene pollen diagram of

Kőris marsh developed on the northern slope of the highest point in the Mátra Mts (near Kékes) suggests that lime formed mixed forests with spruce on the northern slopes of the Kékes between 8400–6100 cal BP, before the appearance of beech (Szabó and Félegyházi 1997, Magyari 2002a). These lime forests obtained their oak forest character probably in the Middle Holocene, when lime was present as an associated species in mixed oak forests at lower altitudes (Willis et al. 1997, Magyari 2002a, Gardner 2002). After the arrival of beech, lime, and probably ash too, survived only in rocky habitats of mountain summits and ridges where beech was competitively inferior (cf. Chytrý and Sádlo 1997). Thus the continental ash–lime forest is likely a remnant from vegetation historical times and represents a former phase of secular succession (Zólyomi 1967). Survival of the ash–lime forests and the formation of specific vegetation mosaic, have also been supported by the influence of continental climate that is apparent in the Északi-középhegység region (Kun 1998). These continental ash–lime forests are regarded as deviations, as opposed to the regularity that such habitats typically foster lime forests similar to oak–hornbeam forests.

3.6 Sphagnum bogs of the northern Nagyalföld and the Északi-középhegység

Sphagnum bogs are exceptionally rare representatives of the boreal vegetation in Hungary, and thus their presence is unexpected and may be regarded as a deviation. Mires provide an opportunity to conduct a rather exact investigation into the question of being relics. *Sphagnum* bogs with *Eriophorum* spp. (and also willow swamps with peat mosses) are preserved in the Mohos Lakes at the northern foothills of the Bükk Mts, and in three lakes surviving in the northern Nagyalföld (106–124 m). We consider as plausible that these bogs originated in the Würm period, and have been continuously present ever since. Indeed, pollen analytical studies found evidence of a mire community similar to brown moss bogs in the layers of 25,000–24,000 cal BP in the Nagymohos Lake, Bükk Mts (Magyari et al. 1999, 2000). Transitional *Sphagnum* mire developed twice during the Pleistocene (25,000–23,000 and 21,000–18,000 cal BP). Macrofossil evidence indicates that several extant species (*Sphagnum palustre, S. magellanicum, Menyanthes trifoliata, Potentilla erecta, Drosera rotundifolia, Carex lasiocarpa)* may be traced back to the Würm period. During the Holocene, stages of open lake, dried mire, floating bog were following one another up to the current stage, and *Comarum palustre, Sphagnum palustre*, and *Sphagnum* sect. *Cuspidatum* were recorded almost in the entire period of 25,000 years (Magyari et al. 2000). In contrast, such continuity from the Pleistocene (or even the Early Holocene) has not yet been supported by evidence either from the Bábtava transitional mire in the northern Nagyalföld or from the Bátorliget fen, both rich in relics but hosting currently no peat mosses (Willis et al. 1995, Sümegi and Gulyás 2004, Magyari et al. 2008). We expect that evidence for the last glacial origin and continuity may be found in the future in one of the *Sphagnum* bogs of the northern Nagyalföld.

4 Uniqueness

Unique features of the natural vegetation are represented by those plant communities that do not occur outside the studied region, hence are endemic to the region as they have unique species composition (Table 3).

The vegetation of the Pannonian region is far from being composed of endemic communities only. Based on their species composition, certain associations could fit into several landscapes of Central Europe. Others may be considered as outliers of the vegetation of neighbouring regions, such as the Illyrian beech forests and oak–hornbeam forests, the rocky grassland with *Festuca dalmatica*, the Carpathian calcareous rock grasslands, and the East Alpine dolomite grasslands. The Pannonian region, however, is not just a simple meeting area of vegetation types from the surrounding regions. Some of the unique vegetation types supporting endemic species developed here by the combination of species typical for the neighbouring regions and yet the unique species composition makes them characteristic for the region. The uniqueness of these communities for the Pannonian region is a dynamic feature. Recent studies on last glacial and post-glacial vegetation changes support the idea that communities continuously disintegrated and reorganised, because the response to climate and consequently the dynamics of species' ranges is greatly species specific ('individualistic'; Bhagwat and Willis 2008, Birks and Willis 2008, Stewart et al. 2010). During the last glacial period, for example, communities very different to those known today developed in the Pannonian region, including tundra steppe (so-called 'mammoth steppe'), macro-ecotone of the tundra steppe and mixed taiga forests, and small pockets of cool-continental broadleaved forests (taiga forest–steppe, see Willis et al. 1995, Magyari et al. 1999, 2000, Rudner and Sümegi 2001, Birks and Willis 2008, Varga 2010).

The most important current endemic plant communities of the Pannonian region are the following:

4.1 Loess forest–steppe forests

The Pannonian forest–steppe forest on loess with *Acer tataricum* of the Nagyalföld and adjacent foothills of the Magyar-középhegység is an endemic zonal vegetation type. This is the dominant potential forest type in the Pannonian loess landscapes in the forest–steppe zone. The sub-mediterranean pubescent oak (*Quercus pubescens*) is a permanent component of the canopy, particularly at the margins of the Nagyalföld. *Quercus robur* and the continental *Acer tataricum* may co-dominate. In the forest interior, and especially along the edges, numerous tall herbs (e.g., *Nepeta nuda* subsp. *nuda, Phlomis tuberosa, Veronica spuria*) and grasses (e.g., *Melica altissima*) are found. In the glades, steppe elements are present in the herb layer (Molnár and Kun 2000). This forest–steppe forest differs by its mesophytic character, more species of oak, and better developed lower forest canopy when compared to similar vegetation dominated by *Q. robur* subsp. *pedunculiflora* and distributed along the lower Danube in Romania and Bulgaria (Zólyomi 1957).

Table 3. Discussed endemic plant communities of the Pannonian region.

Community	Landscape	Main reasons for uniqueness status
Forest–steppe forests on loess	Nagyalföld, Kisalföld and the margins of the Magyar-középhegység	Rare representatives of the sub-mediterranean forest steppe with unique tree composition
Oak scrub forests with *Quercus pubescens* and *Fraxinus ornus*	Magyar-középhegység	Canopy is composed of trees of southern distribution, herb layer is rich in steppe elements
Forest–steppe forests and tall-herb meadow steppes on saline soil	Nagyalföld (Tiszántúl), Kisalföld	Extremely rare forest type; the community of forest glades is the westernmost outpost of an intrazonal vegetation type distributed from Siberia and Kazahstan to Eastern Europe
Forest–steppe forests on sand	Nagyalföld, Kisalföld	Forests close to the climatic forest limit, act as sources and refugia for the montane flora on the continental Alföld
Vegetation mosaic of dry perennial *Festuca vaginata* grasslands with juniper–poplar forests on sand	Nagyalföld, partly on Kisalföld	Edaphic grasslands composed of many endemic species and species of Pontic, Pontic–Submediterranean distribution
Fine-scale mosaic of *Artemisia*- and *Achillea* steppes with *Puccinellia* and *Camphorosma* swards and salt lakes	Nagyalföld, partly on Kisalföld	Presence of numerous Pannonian endemic species and rare species with Pontic–Pannonian, and Irano–Turanian distribution ranges
Open dolomite grassland	Dunántúli-középhegység	Exclusive habitat of several Pannonian endemics and specialists showing southern distribution
Dolomite rocky beech forests	Dunántúli-középhegység	Ecotone-like community with isolated occurrences of species of distant zones and belts (*Allium victorialis, Calamagrostis varia, Carduus glaucinus*)

4.2 Quercus pubescens–Fraxinus ornus and Cerasus mahaleb–Quercus pubescens forests

The dry and warm south-facing slopes of the Magyar-középhegység support a mosaic of low-canopy, open forests (mainly with *Quercus pubescens* and *Fraxinus ornus* in the West and with *Prunus mahaleb* in the East) with dry rock steppes. The trees and most of the shrubs in this vegetation type have southern, mainly Balkan distribution ranges, whereas the herb layer is saturated (especially in the Északi-középhegység) with species showing continental and submediterranean distribution ranges. This special combination of species is what makes our oak scrub forest community endemic or sub-endemic (Jakucs 1961).

4.3 Saline forest–steppe forests

There are other forest types endemic to the Alföld (Hungarian Lowland). Among them is the forest–steppe forests on saline soils found mainly east of the Tisza River. In terms of their origin, some of these forests are ancient, and their stands developed naturally, possibly many thousand years ago. Besides, some of them developed secondarily from hardwood gallery forests in response to lowered groundwater level that followed river regulations in the 19th century (Molnár 1989, Molnár et al. 2012). The vegetation mosaic formed by forest and tall herb communities is unique (Molnár 1989). The species-rich meadow steppes dominated by

Peucedanum officinale and *Galatella sedifolia* are probably the westernmost outposts of an intrazonal tall-forb vegetation type distributed from Kazakhstan and Siberia to Eastern Europe.

4.4 Sand forest–steppe forests

The closed and open oak forests on sand in dry and semi-dry habitats on the extensive Pannonian sandy landscapes are even more distinct from other Central European forests than the saline steppe forests. The separation of the open and closed subtypes has become rather difficult recently because their species composition converges due to the lowered groundwater table, which is caused partly by a long series of drought years since 1984, and partly by excessive water extraction and draining (Molnár et al. 2012). The oak forests on sand (beside the azonal oak–ash–elm riparian forests) are refugia of montane forest flora in the Alföld, including the pubescent oak (*Q. pubescens*; Fekete et al. 2010, Molnár et al. 2012).

All dry oak forests in the Pannonian region are characterised by open canopy. It is particularly characteristic of pubescent oak forests in the Magyar-középhegység having species-rich forest saum and mantle (tall-herb forest fringe and thermophilous scrub, respectively) and are broken by glades occupied by patches of clonally spreading tall herbs (Fekete and Varga 2006). This is an essential difference from the forest-steppe forests of Ukraine and Russia, where the

extensive steppes surround tall, closed-canopy, mesic forests (Lavrenko and Sochava 1956, Berg 1958, Molnár et al. 2008, Didukh et al. 2011).

4.5 Vegetation mosaic on sandy soils

It is not just the forests but the entire vegetation mosaic on sand that is unique (Fekete 1992, Biró and Molnár 1998) to the Pannonian region. On coarse sand the oak forests are replaced by *Juniperus communis–Populus alba–Populus x canescens* forests forming either open-canopy scrub or closed forest, depending on water availability. The juniper–poplar forests form a mosaic with dry sand grasslands on the dunes and grasslands in terrain depressions. The dry perennial sand grassland is a highly edaphically specialised steppe community because the weak water retention capacity of the coarse sand exacerbates the macroclimatic drought for many shallow-rooted species. The dominant species are *Festuca vaginata*, *Stipa borysthenica*, and in somewhat less extreme habitats *Festuca wagneri*. This community hosts many Pannonian endemics such as *Festuca vaginata*, *F. wagneri*, *Colchicum arenarium*, *Dianthus diutinus*, *Iris humilis*, *Sedum urvillei*, *Tragopogon floccosus,* see Electronic Appendix). It occurs mainly on sand between the Danube and Tisza rivers. The other species in this vegetation are mainly Pontic, Continental, or Pontic–Submediterranean floristic elements. In the northeastern part of the Nagyalföld (Great Hungarian Lowland), on acid sands, endemic *Pulsatilla flavescens* occurs. Along the Romanian–Bulgarian section of the Danube and further eastwards in Dobrogea and eastern Bulgaria and southern Ukraine, the dominant grass species is *Festuca beckeri*. Compared to Pannonian sand grasslands, stands close to the seashore in eastern Bulgaria have a more pronounced cryptogamous layer and a greater proportion of long-lived herbs (Rédei et al. 2008).

4.6 Saline vegetation mosaic

The vegetation mosaic on saline soils has unique features (e.g., extension, endemic species and plant communities) in the Pannonian region as well. As anywhere in Eurasia, the fine-scale mosaic is determined by the microrelief, i.e., by the distance to the layer of salt accumulation, and the yearly dynamics of water regime (Tóth and Rajkai 1994, Molnár and Borhidi 2003). On solonetz soils, the short-grass steppes of *Festuca pseudovina* form mosaic with wet swards of *Puccinellia distans* subsp. *limosa*, and dry *Camphorosma annua* patches. Saline swards appear especially in waterlogged habitats and around shallow salt lakes. In the fall, annuals and succulents appear on the dried-out lakebeds. The Pannonian saline vegetation has several dominant species in common with the saline areas of the forest–steppe zone of Eastern Europe (see Lysenko and Rakov 2010) and the zonation patterns along the microtopographic gradients are also similar. However, the spatial proportion of saline grasslands in the landscape is far greater than anywhere else in the Eurasian forest–steppe zone (one–third of the Hungarian grasslands are saline; Molnár et al. 2008). The main reason is geologi-

cal − there are no other so extensive regions rich in elevated (sub)recent floodplain terraces on loess in the forest–steppe zone of Eurasia.

There are several saline plant communities that are endemic to the Pannonian region, such as the *Plantagini tenuiflorae-Pholiuretum pannonici*, the *Artemisio santonici-Festucetum pseudovinae*, the *Agrostio stoloniferae-Beckmannietum eruciformis*, the *Lepidietum crassifolii*, and the *Suaedetum pannonicae*. (The *Cyperetum pannonici* and the *Achilleo setaceae-Festucetum pseudovinae* seem to have subendemic status; P. Eliáš, D. Dité, Z. Melečková, pers. comm.). The vegetation of the extensive saline areas in the Alföld significantly differs from the saline communities on the seashore regarding both the origin of their species and the dynamics of hydrological and geochemical processes. Connection to seashore communities is indicated only by a few species (i.e., *Spergularia maritima*), while related taxa occur frequently (i.e., *Salicornia europaea* vs. *S. prostrata,* see Kadereit et al. 2007; *Bassia hirsuta* vs. *B. sedoides*). The species group of *Suaeda prostrata, S. pannonica, S. corniculata* and *S. salsa* is particularly complicated in taxonomic and evolutionary terms (Freitag et al. 1997, Freitag and Lomonosova 2006, Weising and Freitag 2007). The characteristic species of the Pannonian saline plant communities have, however, frequently Pannonian, Pontic-Pannonian, or Turano-Iranian distribution ranges (see Electronic Appendix). Endemic species and plant communities are indicative of a long evolutionary history of the Pannonian saline vegetation; it may have been a continuous landscape feature of the region since the Würm glaciation through the entire Holocene up to the present (Sümegi et al. 2000, 2005, Molnár and Borhidi 2003). This assertion is also supported by the occurrence of some endemic phytophagous insects (Varga 1989). After all a sizeable area of the Alföld (except for the floodplains and other wetlands) is covered by endemic saline plant communities or their mosaics.

4.7 Open dolomite rocky grasslands

The dry (circum-pannonian) grasslands on Triassic dolomites develop on steep, erosion-prone south-facing slopes and on ridges covered with dolomite rubble. The proportion of sub-mediterranean elements and, accordingly, the proportion of sub-shrubs is high (Futák 1947, Zólyomi 1958). This open-canopy grassland vegetation is dominated mainly by *Carex humilis* and *Festuca csikhegyensis)* and hosts lichen and moss synusia. These communities are the exclusive homes of several Pannonian endemics (*Seseli leucospermum, Dianthus plumarius* subsp. *regis-stephani);* less habitat-specific endemics *(Vincetoxicum pannonicum, Ferula sadleriana, Hieracium kossuthianum)* occur here as well. Furthermore, the single occurrence of the endemic *Linum dolomiticum* was also found in open dolomite grassland.

4.8 Dolomite beech forests

In the same mountainous areas, on dolomite bedrocks, a very unique forest community develops − the dolomite

Table 4. Three criteria of our approach in relation to Heinrich Walter's zonality conceptual framework (incl. discussed examples).

	zonal vegetation	extrazonal vegetation	intrazonal vegetation	azonal vegetation
distributional regularities	pattern of zonal vegetation in the region, (e.g. altitudinal belts in and continentality gradient along the Magyar-középhegység, zonation pattern in Dunántúl, circular zonal pattern on the Nagyalföld)	steppic grasslands on south-facing slopes of Magyar-középhegység	montane closed-canopy mixed forests (*Tilia–Fraxinus*) on limestone	-
distributional deviations (onefold phenomena)	irregular distribution of zonal communities in the Bakony-Balatonfelvidék area	mixed *Pinus sylvestris* forests, cool-continental deciduous forests, (phenomena supported by mesoclimate and edaphic conditions)	montane mixed forests (*Tilia–Fraxinus*) on limestone	*Sphagnum* bogs of the northern Nagyalföld
compositional uniqueness (endemic communities)	zonal forest–steppe forests on loess and sand	-	Alföld: open sand grasslands, juniper–poplar forests, saline vegetation; Magyar- középhegység: *Prunus mahaleb – Quercus pubescens* low forests, dolomite beech forests, rocky dolomite grasslands	hypothetically not impossible

beech forest. These low-grown forests develop mainly on steep north- and north–east facing slopes supporting shallow, skeleton-rich soils. The canopy of these forests is formed by *Fagus sylvatica,* trees of xerothermic sub-mediterranean oak forests (*Quercus pubescens*, *Fraxinus ornus)*, and sometimes by *Sorbus* (*S. aria*, *S. torminalis*, and their hybrids). In the shrub layer *Cotinus coggygria* is the most prominent element. *Carex alba* is a frequent ground-layer graminoid, and *Allium victorialis*, *Carduus defloratus* subsp. *glaucinus*, *Festuca amethystina, Primula auricula* etc.) are possibly relics from the last glacial period (Zólyomi 1958, Isépy 1970).

4.9 Uniqueness: summary

It seems that Pannonian endemics are linked to a greater variety of communities (dry grasslands, rock grasslands, sand steppes, saline meadows, xero-thermophilous forests) than the do the broadly distributed Pontic–Pannonian species (see the Electronic Appendix). The diverse (spanning South-Siberian to Balkan elements) biogeographical affinity of taxa in Pannonian rock grasslands is particularly noteworthy. The Pontic–Pannonian species, on the other hand, contribute to the species pool of the steppe vegetation to a much greater extent than do the Pannonian endemics.

References to the original descriptions of the vegetation types discussed above (and some other, more locally distributed endemic ones) can be found in the synthetic works cited at the beginning of this paper. Our view have been to a large extent influenced by research undertaken outside Hungary, in the neigbouring Slovakia, Austria, Romania, and former Yugoslavia (e.g., see Michalko 1957, Niklfeld 1964, Holub et al. 1967, Horvat et al. 1974, Jovanović et al. 1986, Michalko et al. 1987, Karrer and Kilian 1990, Ivan et al. 1993, Mucina et al. 1993, Csiky 2004, Roleček 2005, Chytrý 2007, 2009, 2011, Willner and Grabherr 2007, Illyés et al. 2009, Dúbravková et al. 2010, Eliáš et al. 2013).

5 The RDU framework and Heinrich Walter's zonality theory

Phenomena assessed by the three criteria of our RDU framework can be further analysed in the light of H. Walter's zonality/azonality framework, as both describe geographical phenomena of large-scale vegetation patterns. The summary of this comparison is presented in Table 4.

According to Walter's theory zonal vegetation patterns develop under the control of macroclimate rather than by edaphic factors (for the European scheme of the zonal vegetation see Mucina 2013). Extrazonal communities are representatives of a particular vegetation zone but are found outside that zone. Azonal vegetation patterns are controlled primarily by other than macroclimatic factors, such as special soil conditions, salinity, water flooding and waterlogging, hence this vegetation need not be restricted to particular zones (Walter and Straka 1970, Walter 1973, 1976, Walter and Breckle 1991; Rutherford et al. 2006). In the Russian and Hungarian literature (also see Rutherford et al. 2006) the term intrazonal vegetation is also used for those edaphic vegetation types that show a close association with a particular zone (see e.g., Jarosenko 1961, Zólyomi 1967).

The two frameworks are independent from each other. Walter's framework is a more or less homogenous system building on a few guiding principles. The RDU framework

is deliberately a non-homogenous, mixed system built both on non-spatial properties (e.g., composition and history) as well as spatial ones, such as altitudinal distribution, sequence of zonal communities in space, and their shift along macroclimatic gradient. The RDU framework addresses finer scales of spatial complexity (regions, landscapes). Our paper documents that the two frameworks give complementary explanation of vegetation spatial phenomena on meso- and macroscales.

6 Conclusions and outlook

In this paper, we introduced a new conceptual framework (RDU) aimed at assisting analyses of vegetation patterns at the region scale, and applied this framework to the Pannonian region. We shortly tackled the regularities of vegetation patterning discussing of zonal plant communities, in particular patterning of altitudinal belts, the basin effect of the Nagyalföld, and the effect of the increasing continentality to the East. Examples of deviations were found in most altitudinal belts, and in both the broadleaved forest and the forest–steppe zones. Apparently, deviations developed mostly as a response to mesoclimate, special local edaphic situations, or as a consequence of special local vegetation history. We enumerated the most important endemic plant communities representing unique features. Most of them occur in the lowlands or on the south-facing slopes of the mountain ranges fringing the central lowland part of the Carpathian Basin. The high amount of endemism is likely to be attributed to the fact that the Pannonian region was characterised by transitional climate during nearly the whole younger Quaternary. Transitional climates likely enhanced the relic-preserving processes, mostly through supporting a diversity of ecotones (Varga 2010). This assumption is supported by the observation that relic species (often species with island-like occurrences representing distant vegetation zones) prefer ecotones today (see Zólyomi 1987 for examples). Zólyomi (l.c.) also devised a method for recognising relics that uses the relative position (TWR indicator value) of vegetation relevés along three axes (T: temperature, W: water, R: acidity). The relevés containing relics show a transitional character along the axes of the above-mentioned indicators.

We suggest that our new conceptual framework could be applied to the analysis of other biogeographical regions, eventually allowing for inter-regional comparisons. It is more than likely that the weight and importance of each of our three criteria will be different in different geographical set-up. We present a potential example of such a comparison. The most closely related region to the Pannonian region is the area along the lower reaches of the Danube (Wallachia north of the Danube and a narrow strip of northern Bulgaria along the southern banks). This area borders on the Southern Carpathians in the north, on Dobrogea in the east, and on the mountain ranges of the Balkans (Stara Planina) in the south and in the southwest. Some of the Pannonian endemic and sub-endemic communities (open perennial grasslands on sand, saline steppes, loess steppes and loess forest–steppe forests) are closely related to the geographically analogous vegetation types occurring here. The pattern of vegetation

belts is also similar at the first sight (Doniţa et al. 1960, Niklfeld 1974, Ivan et al. 1993, Bohn et al. 2000). However, the zones along the lower reaches of the Danube are driven by slightly different rules. In the zone of oak forests – and even in the forest–steppe zone – the number of separate vegetation units is greater. Individual communities form clearly distinguishable additional sub-belts (Bohn et al. 2000) characterized by dominance of one or two oak species (Georgescu and Constantinescu 1945). Mesophilous forests of Central-European tree species (primarily beech and hornbeam forests) are present, but their low-altitude border is located at higher altitudes than in the Pannonian region, which is an indication of the reduced vitality of beech and hornbeam compared to oaks. The development of such oak sub-belts is not found in the Pannonian vegetation. Deviations also play a role in differentiating the Pannonian and Wallachian regions. There are Pannonian vegetation types (even at the landscape scale) that may have survived since the Early Holocene. We are not aware of similar relics, deviations in the region along the lower Danube.

Naturally, biogeographical aspects also emerge in such comparisons, since vegetation geography is part of biogeography. Biogeography classifies spatial units according to their individual features. This is a similar process, whether the whole biota or only vegetation is concerned. The *vegetation-geographical region* is a variant of the *region concept*, an analogy to the 'vegetation-landscape' concept (see e.g., Zonneveld 1990). The definition of the biota typically follows a reductionist route as illustrated by studies delineating a region by the distribution of a single taxonomic group (e.g., Vargas et al. 1998, Marquez et al. 2001, Rojas-Soto et al. 2003).

We demonstrated the usefulness of paleobiological (palynological) evidence in explaining phenomena of recent vegetation, the deviations in particular. With increasing density of sampling locations, the amount of information about local vegetation history is supposed to increase considerably. We expect to gather more insight especially on the processes that might have lead to the appearance of specific vegetation-pattern deviations. Consequently, palynology is expected to become a more relevant tool and source of information for vegetation scientists studying current vegetation patterns (see for instance Molnár et al. 2012). Reconstruction of palaeo-vegetation zones (pollen-based biomes) will be possible, and – in certain cases – it will also be possible to interpret the chorological phenomena of individual species (such as disjunctions, as shown by Strong and Hills 2005).

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Electronic Appendix

Pannonian endemics (and subendemics) and Pontic–Pannonian (and sub-Pontic-Pannonian) flora elements found in the Pannonian region based on Euro+Med (2006-2013). The file may be downloaded from the web site of the publisher.