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Points of View

Delineation of the Pannonian vegetation region

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Abstract: Phytogeographical regions have been set up traditionally on the basis of the flora. Several examples indicate that the potential natural vegetation is also suitable for this purpose although the flora- and vegetation-based boundaries do not necessarily overlap. We define a vegetation region as an area where the physical geographic features are rather uniform, and which consists of landscapes with floristically/structurally similar vegetation and/or their repetitive mosaics. In this paper, we delimited the boundaries of the Pannonian region based on the distribution of characteristic plant communities. The line runs most often on the border between *Quercus cerris-Quercus petraea* and *Carpinus betulus/Fagus sylvatica* dominated landscapes. We provided descriptions of the potential vegetation on both sides of the boundary. The region has an area of 167,012 km^2. The region is either in direct contact with the neighboring regions (e.g., Western Carpathians), or is separated from them by transitional areas (towards the Eastern Alps), and character-poor areas with non-Pannonian, non-Alpine, non-Dinaric vegetation (in the southwest to the Western Balkan). Often, the boundary does not coincide with the boundary of the Pannonicum floristic province. We found that vegetation region boundaries can help reevaluate long-established floristic region boundaries. The boundary of the 'floristic Pannonian region' also requires revision based on integrated distribution databases and statistical analyses. We argue that the method applied here is simple, repeatable and falsifiable. Our map provides an opportunity to the European Union to use a scientifically more sound biogeographical circumscription of the Pannonian region in her Natura 2000 and other programs.

Introduction

Phytogeographical regions have been set up traditionally on the basis of the flora of the studied area (Walter and Straka 1970, González-Orozco et al. 2014). Thus, the boundaries are the function of the geographic distribution of a large number of species – which rarely coincide. One has to select a subset of species to be used, but the choice is not entirely without subjective decisions. It would be therefore useful to use a simpler and more objective method for biogeographic regionalization. Several example indicate that vegetation is suitable for this purpose (Schmithüsen 1968, Schubert 1991, Hegg et al. 1993, Bailey 2005, Zhang 2007, Molnár et al. 2008a etc.). Dierschke (1994) discussed delimitations based on vegetation and terms such as vegetation sector, vegetation province, vegetation region, etc. (see also Schmithüsen 1968). Larger spatial units of „vegetation areas" (Vegetationsgebiete) may be composed of spatially neighboring smaller units that have their own characeristic plant communities and their complexes, furthermore specific floristic and physiognomic features, e.g., endemic taxa, related formations (Dierschke 1994). A biogeographical region defined by its vegetation (hereinafter vegetation region) is an area above the landscape scale, where the physical geographic features are rather uniform and which consists of landscapes with floristically and structurally similar vegetation and/or repetitive mosaics of such landscapes (Fekete et al. 2014).

The delimitation of vegetation regions has often been based on maps of the potential natural vegetation (e.g., Küchler 1985). Bailey (2005) used vegetation beside climate when drawing the ecoregion map of the United States. The biogeographical regionalization of China is also based on vegetation (Zhang 2007). The biogeographical division of Europe has been completed on the basis of plant communities and vegetation complexes (Schubert 1991). Vegetation-based geographical division of countries into smaller units is available in Switzerland (Hegg et al. 1993) and Hungary (Molnár et al. 2008a).

The Pannonian floristic province (Pannonicum) is a widely accepted biogeographical region in Central Europe, a separate unit in phytogeographical maps prepared at different scales (e.g., maps of Eurasia: Meusel et al. 1965, Meusel and Jäger 1992, maps of Europe: Soó 1932, 1965).

It covers the inner parts of the Carpathian basin reaching out from the Basin only in north-west. The Carpathian Basin is characterized by a great wealth of floristic elements from different parts of Eurasia. In addition to the broadly distributed Eurasian species, the proportion of sub-Mediterranean, continental, Pontic and Balkanian species is also substantial. Its floristic distinctiveness comes from the combination of these floristic elements, as well as the occurrence of Pannonian endemics. Delimitation of the Pannonicum was attempted first by Kerner and Wettstein (1888), Borbás (1905) and Rapaics (1910). Jávorka (1924–1925) and Soó (1933, 1945, 1947) prepared the first detailed cartographic delimitation of the region (Fig. 1).

It seems likely that the sections of the boundary of the Pannonicum floristic province running across eight countries were not delimited by the same precision. Thus, the floristic boundary should be revised in the future using standard methodology and a fixed scale. New enumerations of local floras and the new modern flora databases could effectively help this work. However, determination of the boundaries of the Pannonicum floristic province with sufficient precision is likely to be a long and laborious process. We argue that using vegetation as a basis for the delineation of the Pannonian region would be quicker and more homogenous in content. We accept, however, that the flora and vegetation-based boundaries of the region do not necessarily overlap.

The vegetation of the Pannonicum has been characterized recently by Fekete et al. (2014) based on three newly developed concepts: distributional regularity (e.g., the altitudinal pattern of vegetation belts, and the gradient of continentality along the mountain ranges), distributional deviation (the conspicuous departure of vegetational phenomena from the expected pattern expressed as regularity), and compositional uniqueness (e.g., the endemic zonal forest–steppe forests and intrazonal endemic communities). Following these concepts, we describe the boundaries of the Pannonian vegetation region. We use the term vegetation region in a broad sense not specifying it in a hierarchical order (Dierschke 1994).

The vegetation-geographical delimitation of the Pannonian region proved to be timely and possible for several reasons. On the one hand, almost all affected countries have completed their own maps of the potential vegetation (Hungary: Zólyomi 1989, Slovakia: Michalko et al. 1984-1986, Yugoslavia: Jovanović et al. 1986, Romania: Ivan et al. 1993; a countrywide mapping of current habitats has also been completed in Hungary, see Bölöni et al. 2008, Molnár et al. 2008b), and simultaneously, large amounts of geobotanical information have been accumulated in these countries. On the other hand, the European conservation authorities in their Habitat Directive drew an imprecise and thus misleading boundary of the Pannonian biogeographical region, particularly in the west and the south, where the boundary runs along the border of the European Union of the time (Anon. 2014, Fig. 1). This also has motivated us to develop a more scientifically sound method and come up with a more accurate boundary line.

Materials and methods

Data sources of delineation

In drawing the boundary of the Pannonian vegetation region, we used maps of the potential vegetation and local vegetation descriptions, in addition to our own field experience:

1) map of the potential natural vegetation of Hungary (1: 1,500,000, Zólyomi 1967, 1989) and works on the vegetation of the border zone (e.g., Zólyomi 1941, Jeanplong 1956, Pócs 1960);

2) map of the natural potential vegetation of Czechoslovakia (1: 200,000, for Slovakia: Michalko et al. 1984-1986, and for the Czech Republic: Mikyška et al. 1968-1972) and the attached explanatory text (Michalko et al. 1987), and an earlier 1: 500,000 scale map for Slovakia (Michalko et al. 1979);

3) map and description of the natural potential vegetation of Yugoslavia (Fukarek and Jovanović 1986);

4) map of the potential vegetation of Romania (Ivan et al. 1993);

5) map of the natural vegetation of the countries along the Danube river (1: 2,000,000, Niklfeld 1974);

6) map of the potential vegetation of Europe (1: 25,000,000, Bohn et al. 2000);

7) distribution maps of current habitats derived from the Hungarian habitat mapping database (Molnár et al. 2007, Molnár et al. 2008b, Bölöni et al. 2008), habitat descriptions (Bölöni et al. 2011), and descriptions of geographical microregions of Hungary based on the flora and vegetation (Király et al. 2008), and finally

8) vegetation descriptions, phytosociological tables from the margins of the region (see references mentioned above).

Pannonian plant communities of the study area

To determine the boundaries of the Pannonian vegetation region, we used plant communities that are regarded typical for the interior of the Carpathian Basin, and thus are considered Pannonian (Fekete et al. 2014).

They include the still widespread and climatically zonal or edaphic communities and also intrazonal communities, which occur within the belt of these vegetation types. The Pannonian character of the communities was assessed with the help of the rich phytosociological literature. In the descriptions below, the names of plant communities follow Borhidi et al. (2012). For more detailed descriptions, see Borhidi et al. (2012) and the publications listed in the references. Nomenclature of flowering plants follows Király (2009). Geographical names used in the text are given in the local official language or in English. The most extensive Pannonian communities are as follows:

Oak steppe forest on loess with Acer tataricum: the climatically zonal forest community on the lower foothills of the mountain ranges bordering the Great Hungarian Plain and on the loess-covered parts of the latter is *Quercetum pubescenti-*

roboris. This community is a representative of the sub-Mediterranean variant of the forest steppe vegetation. The co-occurrence of *Quercus robur* and *Quercus pubescens* as forest dominants (unlike in Eastern Europe) and the frequency of their hybrids are a Pannonian feature. *Acer tataricum* may often form a lower forest canopy layer. The herb layer includes several forest-steppe species of tall forbs. The grassland component of the forest steppe is represented by species-rich meadow steppe (i.e., *Salvio nemorosae-Festucetum rupicolae*, *Euphorbio pannonicae-Brachypodietum pinnat*i).

Oak steppe forests on sand: these xeric and xeromesic oak forests are restricted to extensive sandy regions and are unique to the Carpathian Basin. The rather closed types *Convallario-* and *Polygonato latifolii-Quercetum roboris* and the somewhat open *Festuco rupicolae-* and *Iridi variegatae-Quercetum roboris* communities require the presence of groundwater within reach of roots. The most open type of woody vegetation is *Junipero-Populetum albae* on the driest sand dunes.

Open sand steppe: formed by *Festucetum vaginatae* community with *Stipa borysthenica* and *Festuca wagneri* at places. The number of Pannonian endemics (mainly on the sand between the Danube and Tisza rivers) is the highest in this community. Many of its common species have Pontic, Pontic-sub-Mediterranean and continental range of distribution.

Oak steppe forests on solonetz soil: The typical open forest of the forest steppe with a mosaic-like structure (community *Galatello-Quercetum roboris*) is almost unknown in other parts of Europe. The vegetation in the glades (*Peucedano-Asteretum sedifolii*) is the westernmost representative of an intrazonal vegetation type distributed from South Siberia as far west as East Central Europe.

Halophytic herbaceous vegetation: Halophytic grasslands and marshes are widespread in the Pannonian region (e.g., *Artemisio santonici-Festucetum pseudovinae*, *Agrostio stoloniferae-Alopecuretum pratensis*, *Lepidio crassifoliae-Camphorosmetum annuae*, and *Puccinellietum limosae*). The Pannonian halophytic vegetation greatly differs from the saline maritime communities of European coastal areas in both soil development and dynamics, as well as in the origin of species. The distinction is further amplified by the occurrence of some endemics. The majority of the characteristic species have Pontic-Pannonian and even Irano-Turanian range of distribution.

Hardwood riparian forests: The potential vegetation types on the high-lying parts of the floodplains along lowland rivers are *Fraxino pannonicae-Ulmetum* and its allies. The Pannonian character is due mostly to the occurrence of *Fraxinus angustifolia* subsp. *pannonica* and *Acer tataricum*.

Forests of Quercus petraea-Quercus cerris: The most widespread zonal forest community on the low hills and lower mountain regions in the Pannonian region is *Quercetum petraeae-cerridis*. One of the dominant species, *Quercus cerris*, has an eastern sub-Mediterranean area of distribution, and is an indicator of climate. The northern boundary of its distribution range (Fekete and Blattny 1913) within the Carpathian Basin fits well the "Moesz-line", which is the northernmost limit for the distribution of Pannonian species and also grape cultivation (Moesz 1911). The constant species in the *Quercetum petraeae-cerridis* are mostly sub-Mediterranean, sub-Mediterranean-Central European, and Pannonian-Balkanian species. The co-dominant tree in the community is the Central European *Quercus petraea*. The co-dominance of the two oak species clearly attests the transitional character of the Pannonian region. In terms of floristic composition, the *Quercetum petraeae-cerridis* shows some intermediate features between the Sarmatian *Potentillo albae-Quercetum roboris* and the northeast Balkanian *Quercetum farnetto-cerridis* (Soó 1963). It is a distinct Pannonian community despite the absence of Pannonian endemisms, which differs from both communities above, although it is more closely related syntaxonomically to the latter one. These forests were once directly adjacent to the *Quercetum pubescenti-roboris* forests of the forest steppe, and they may share numerous Eurasian, south and southeast European, continental and Pannonian-Balkanian species that are characteristic of the Festuco-Brometea class (Kovács 1975, Kovács and Podani 1979).

Despite the most recent phytosociological classification (Borhidi et al. 2012), we consider the related *Asphodelo-Quercetum roboris* community (Borhidi and Járai-Komlódi 1959, Tallós 1959, Kevey 2008, 2011) Pannonian rather than Illyrian. In addition to the occasional occurrence of a few sub-Mediterranean, sub-Atlantic-sub-Mediterranean and Illyrian species, it shares several dozens of species with the zonal Pannonian *Quercetum petraeae-cerridis* forests. The *Agrostio tenuis-Quercetum cerridis* community (Csapody 1974) is similar, but without any Illyrian character (Kevey 2008, Király and Király 2008). Both communities bear some forest-steppe features as well (Zólyomi 1941, Borhidi and Járai-Komlódi 1959, Kevey 2011).

The Pannonian character of the *Quercetum petraeae-cerridis* belt is further accentuated by the presence of intrazonal edaphic and often endemic communities. The most widespread of them are Pannonian oak scrubs (*Cotino-Quercetum pubescentis*, *Ceraso mahaleb-Quercetum pubescentis*) growing primarily on dry and warm limestone and dolomite hillsides. They are characterized by an open, mosaic-like structure with glades, stunted growth of *Quercus pubescens* and *Fraxinus ornus*, and high species richness in the forest margin ecotones. The main forest trees and many of the shrubs are species growing mainly in the Northern Balkan, whereas the herbaceous component is also rich in continental steppe elements. This dual character is a Pannonian feature (Fekete et al. 2014). The dolomitic rock grassland (*Seseleo leucospermi-Festucetum pallentis)* exclusively hosts several Pannonian endemics. Other less widespread Pannonian communities are *Waldsteinio-Spiraeetum mediae*, *Tilio-Fraxinetum excelsioris*, *Poetum scabrae*, and *Campanulo macrostachyae-Stipetum tirsae.*

Method of delineation

The boundary line of the Pannonian vegetation region was drawn onto the map of the natural vegetation of Europe

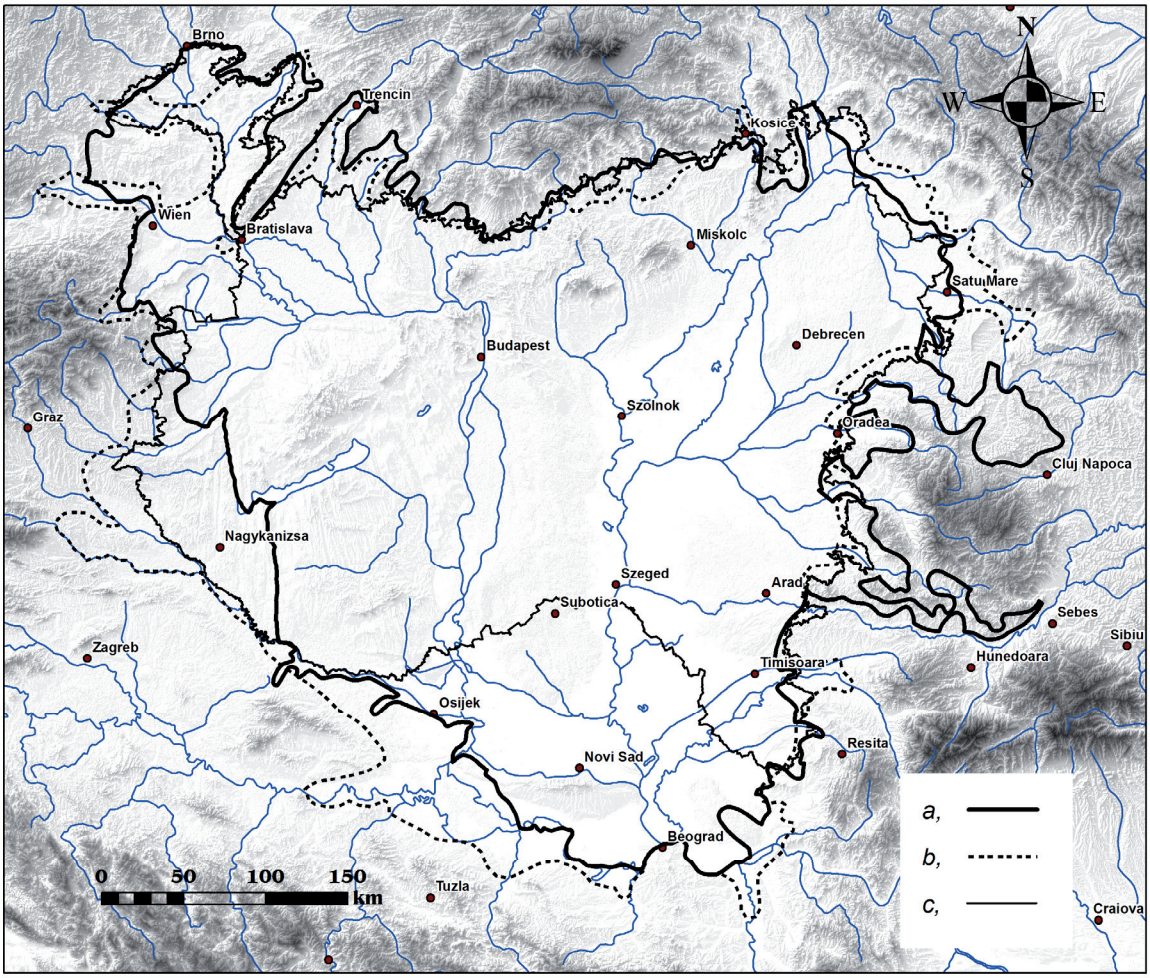

Figure 1. The boundary lines of the a) Pannonian vegetation region; b) the Pannonicum floristic region based on latest version covering the whole region (Soó 1947); and c) the Pannonian biogeographic region of the European Union (Natura 2000, Anon. 2014, note: it often runs on country borders) (source of base map: ASTER-GDEM, 2009, NASA).

(Bohn et al. 2000). On this map, all the important zonal Pannonian communities are identifiable.

First, we drew a preliminary line along the external border of the areas with Pannonian vegetation. This was followed by a detailed test. Information for this test came from finer-scale maps, a large number of vegetation descriptions, and our own personal field observations at places. We checked the base map patch by patch whether patches were identified and their borders were drawn correctly, and whether merging certain patches on the map were justifiable. The final boundary line was established after completing all the necessary corrections.

We considered an area as part of the Pannonian vegetation region if Pannonian vegetation types covered more than 50% of it, or if azonal vegetation was predominant and non-Pannonian vegetation types (like *Fagetalia*-communities) took up a negligible portion of the vegetation. In most cases, the boundary was drawn along the outer margin of the geographical range of a Pannonian community, usually between *Quercetum petraeae-cerridis* communities and forests dominated by *Carpinus betulus/Fagus sylvatica*.

In cases when a Pannonian community or vegetation complex fully surrounded smaller areas mostly dominated by *Carpinus betulus/Fagus sylvatica* forests, the latter were included in the Pannonian vegetation region (these isolated occurrences of non-Pannonian vegetation were not indicated on our maps).

When an area between two vegetation regions was occupied by azonal riparian vegetation, we arbitrarily set the boundary along the current course of the river. If an adjoining area did not show characteristic features of a vegetation region, but was covered with vegetation other than riparian communities, we set the boundary on its adjoining edge. In case of some ambiguous sections, we consulted local and regional experts. For every boundary section, we provided the names of the typical vegetation types on both sides and the related references. The neighboring vegetation regions were neither analysed, nor named. They have to be defined on their own merits.

Results and discussion

The boundary line of the Pannonian vegetation region is shown in Fig. 1 (for GIS files see the Electronic Appendix).

The northern boundary

The once extensive oak steppe woodlands in the Kisalföld and the Podunajská nížina (Horváth-Godány 1977) and the loess-covered area north of them are replaced further north by *Quercetum petraeae-cerridis*. This community forms the boundary of the Pannonian vegetation region here. Oak forests north of this line are represented by the related, but non-Pannonian *Potentillo albae-Quercetum roboris* (Bohn et al. 2000, Roleček 2005).

In the Váh valley and between the Biele Karpaty and Malé Karpaty, the Pannonian vegetation is represented by the sub-Mediterranean *Cotino-Quercetum pubescentis* (Futák 1947, Jakucs 1961, Michalko et al. 1987, Chytrý 1994). Elsewhere, as a response to microclimatic and/or edaphic influences, continental xerothermic oak forests (*Corno-Quercetum pubescentis*) play the same role (Roleček 2005). These xerothermic forests do not penetrate to the north farther than the zonal Pannonian xeromesic closed oak forests. In the Ondava valley, the boundary is determined by the northern limits of *Quercetum pubescenti-roboris* within the Pannonian vegetation region. From the direction of the Northwestern and Northern Carpathians, the northern boundary, almost in its full length, is bordered by *Carici pilosae-Carpinetum* and, in exceptional cases, the related *Tilio-Carpinetum* (Michalko et al. 1984-86).

The north-western boundary

In the southeastern part of Moravia, the boundary of the Pannonian vegetation region again is determined mainly by the distribution limits of *Quercetum pubescenti-roboris* forests growing mostly on gentle loess slopes (Chytrý and Horák 1997) and alternating with meadow-steppe patches. In the Pannonian part of Moravia (cf. Kaplan 2012), a supposedly endemic community (*Carici fritschii-Quercetum roboris*, Chytrý and Horák 1997) has been described as a close relative of some *Quercus robur*-dominated open grassy oak forests in Hungary. Additional evidence of the Pannonian character is provided by the presence of large stands of *Inulo hirtae-Stipetum tirsae* (Dubravková et al. 2010), and the once species-rich, but now extinct or fatally degraded *Thero-Salicornietea* communities (Chytrý 2012). Our boundary line in Moravia approximately follows the line proposed by Chytrý (2012). The so-called Pannonian (sub-Pannonian) mesic *Quercus robur-Carpinus betulus* forests are widely distributed in the plains and broad valleys between hills in the warm and sub-continental parts of Slovakia, Austria, and Bohemia (Czech Republic) (Michalko et al. 1987, Mucina et al. 1993). These forests (named as *Primulo veris-Quercetum roboris*, *Polygonato latifoliae-Carpinetum,* etc.) are representatives of the forest-steppe zone and also the zone of *Quercetum petraeae-cerridis*. They rarely extend beyond the boundary defined by the distribution limits of Pannonian oak-woods.

The Pannonian vegetation of southeast Moravia continues to Niederösterreich, Marchfeld, the Wiener Becken, and Northern and Central Burgenland (for details, see Kilian et al. 1994, Niklfeld 1993, Willner 2013). In the lowlands and the adjacent foothills, the Pannonian vegetation with halophytic and sand steppe communities and with heavily eroded loess hillsides was richly represented in the potential vegetation (Hübl and Holzner 1975). The dominant vegetation type was *Quercetum pubescenti-roboris* on the lowlands, and *Quercetum petraeae-cerridis* (Geeerdes and Moll 1983, Karrer and Kilian 1990, Wallnöfer 2003, etc.) on the low hills. The *Quercus petraea-Q. cerris* belt is also rich in Pannonian communities, such as basiphilous rocky vegetation (Niklfeld 1964), xerothermic oak scrub (*Ceraso-Quercetum pubescentis*) and closed *Quercus pubescens* forest (*Corno-Quercetum pubescentis)* (Karrer and Kilian 1990, Wallnöfer 2003, etc.). In Niederösterreich, the boundary separates the *Quercetum petraeae-cerridis* on the eastern side from the Central European *Carpinus betulus*/*Fagus sylvatica*-dominated forests (e.g., *Carici pilosae-Carpinetum* and *Primulo veris-Carpinetum*), and occasionally the Hercynian *Potentillo albae-Quercetum roboris* on the western side. The Sarmatian and Pannonian oak forests in Niederösterreich may also form transitional stands (Hübl and Holzner 1975, see also Horvát 1980, 1981, Geerdes and Moll 1983, Mucina et al. 1993).

The western boundary

South of the Leithagebirge, the boundary lies on the eastern edges of the Soproni-hegység, then turns back into Austria. In some places in Central Burgenland the vegetation is also of Pannonian character. More to southeast, the boundary line on the lower hilly areas (Répce- and Gyöngyös-sík, Kemeneshát) is defined by *Cyclamini-Carpinetum* (cf. Zólyomi 1967, 1989) on the western side. In addition to the presence of the zonal Pannonian *Quercetum petraeae-cerridis* forests, the eastern side of the boundary is characterized by the local occurrence of the *Agrostio tenuis-Quercetum cerridis* (on the Répce-sík and Kemeneshát, Csapody 1974) and the *Asphodelo-Quercetum roboris* (Borhidi and Járai-Komlódi 1959, Kevey 2011) communities, the latter extending from Somogy county, both occurring there for edaphic reasons. In the eastern Zala Hills, which form the western boundary, already *Fagetalia* communities dominate. Reaching the line of Lake Balaton (in the area of Keszthely), the border follows the riparian forests and marshes in the Zala river floodplain. In the western part of Somogy county, the boundary is drawn in the center of the transitional zone between the Illyrian *Carpinion* and *Aremonio-Fagion* forests and the Pannonian *Asphodelo-Quercetum roboris* extending as far south as the Drava river.

The southern boundary

The boundary is arbitrarily set as the Drava and Danube rivers in the southeastern part of Dunántúl. Along the south-

ern boundary, the Pannonian character is most clearly represented by forests of the forest-steppe, which are typically open with numerous steppe elements, similar to the vegetation in the more northerly Vojvodina (Jovanovic 1997, Purger et al. 2014). The sand vegetation also defines the boundary. Pannonian species are richly represented in it, although the Balkan *Tilia tomentosa* is already co-dominant in the forests, and some southern elements also appear in the herbaceous vegetation, primarily in the well known Deliblatska Peščara (Gajić 1983). The infiltration of Balkan species in the forest-steppe forests in the more northerly Fruška Gora is already apparent (Jovanovic 1997).

More or less east of the Drina River, the boundary is defined by the partially edaphic *Carpinus betulus-Quercus robur* forests from the south. Elsewhere, the boundary is demarcated by the Illyrian-west-Moesian *Quercus farnetto-Quercus cerris* forests extending from the south (Jovanovic et al. 1986). Compared to the northern and northwestern sections of the boundary, an important difference is that the Pannonian *Quercetum petraeae-cerridis* community is absent here.

The eastern boundary

The south-eastern boundary is formed by the plant communities of the zone of the Pannonian forest steppe. They are adjacent to *Quercus farnetto, Q. cerris* forests covering the hilly areas of foothills of the mountains bordering the Câmpia de Vest plain. North of the Mureş River, in the valley of the river up to Câmpia Transilvaniei on the western and northwestern flanks of the Munţii Apuseni, and on the hills along the Someş River the boundary is determined by the stands of Quercetum petraeae-cerridis (Pop et al. 1978, Csűrös 1981, Ardelean 1999).

It has been recently recognized that the latter is one of the most extensive forest type in the Dealurile Tăşnadului, occurring zonally between 200 and 350 meters a.s.l. These forests are largely similar in species composition to those in Hungary (Karácsonyi 2010, 2011).

Thus, we drew the eastern boundary along the external margin of the cartographical representations of this forest community. This line strongly deviates from the boundary line established by phytogeographical (floristical) analyses. On the eastern side, it is bordered in the Munţii Apuseni, on the hills along the Someş River, and in the area south of the Mureş Valley by mesic deciduous forests, *Quercus robur* forests and communities dominated by *Carpinus betulus* and *Fagus sylvatica*, and oak forests with *Quercus petraea*, respectively (Ivan et al. 1993). After all, the intrusion of the Pannonian vegetation in the interior of Transylvania is best marked by the gradual disappearance of the sub-Mediterranean component, mostly *Quercus cerris* (Negulescu and Savulescu 1957).

In the northeast, the boundary of the Pannonian vegetation region was drawn on the arbitrary line of the Tisza and Bodrog rivers, in the middle of the broad floodplain. Here and east of this area, Pannonian vegetation types are scarce and cover only small areas, such as a narrow strip of xeromesic oak forests on the edge of mountains (Niklfeld 1974, for description see Didukh et al. 2011) and on the dry foothills rising from the plains (Fodor 1960).

In summary, the boundary of the Pannonian vegetation region runs along mostly the hills and low mountains surrounding the Great Hungarian Plain. The area of the region is 167,012 km^2. Areas of considerable size with Pannonian vegetation types do not occur outside of the region boundary. We considered parts of the Északi-középhegység where *Carici pilosae-Carpinetum* and *Melittio-Fagetum* communities dominate the landscape (e.g., Börzsöny, Bükk, Mátra Mts.), and the Mecsek and Zselic Hills, as well as the Fruška Gora in the south as isolates, and thus these are not indicated in the map. The longest stretches of the boundary of the vegetation region (Northern Carpathians, Weinviertel, Transylvania) run along the external margin of *Quercus cerris-Quercus petraea* forests. Oak steppe forests on loess and sand, sand steppes and floodplain forests are less important in demarcating the boundary line.

The boundary of the Pannonian vegetation region is often surprisingly sharp, especially where landforms change abruptly (plain-hill country) which is often accompanied by a change in bedrock. At higher elevations, Pannonian oak woods are replaced by *Carpinus/Fagus*-dominated forests. The sharpness of the boundary in such cases is due to the low-light environment in the mesic oak-hornbeam forest, which is not conducive to photophilous species in the *Quercetum petraeae-cerridis* oak wood, but is favorable to the mountain flora. The width of the boundary may be in the order of few meters at places ("limes convergens", Dierschke 1994). Note that the floristic boundaries tend to be broader. The boundary between the Pannonicum and Alpicum in the Soproni-hegység, for instance, is a series of floristic steps within a 2-3 km broad zone, rather than a sharp line (Király and Szmorad 2004). Similarly, a 1–2 km wide transitional zone was detected along the boundary of Pannonicum and Hercynicum. There are several taxa in this transitional zone that are also present either in the Pannonicum or Hercynicum (Chytrý et al. 1999). In the hill country lying along the boundary between Pannonicum and Dacicum (Eastern Carpathians) (Sălaj), the transition zone is particularly broad, where gradients of Pannonian, Pontic-Pannonian and Pontic-sub-Mediterranean species towards Câmpia Transilvaniei were observed (Karácsonyi and Negrean in litt.).

Areas with transitional or uncharacteristic vegetation between vegetation regions

The boundary line in the western section runs along an extensive transitional hilly area that is in contact with the East Alpine vegetation region in the west. This transitional character is shaped by influences from the two neighboring regions, and also those of the West-Balkan, the latter of which manifesting themselves in the species composition of the extensive *Carpinus-Quercus* and *Fagus* forests (Pócs 1960). An additional feature of the area is the presence of patches of mixed forest with *Pinus sylvestris* (*Genisto nervatae-Pinetum*

sylvestris) with associated vegetation complexes, which are regarded as the extant representatives of the once continuous southern boreal European forest zone, relics of the early stages of postglalcial forest development (Pócs et al. 1958, Pócs 1960), which were not replaced later by broadleaved forests. It is this peculiar mix of vegetation types and the transitional character that render this large area confined between two vegetation regions a certain degree of uniqueness. Therefore, we regard it as being significantly different from either of the two neighboring (East Alpine and Pannonian) vegetation regions.

That the transitional zones between vegetation-based ecoregions may be rather broad is advocated by Bailey (2005) with examples (see also Küchler 1973). The existence of transitional and character-poor areas is also recognized in geographical landscapes where transitions regularly develop as well (Kádár 1965, for overlapping and noncomplementary landscapes, see Kádár 1941).

More generally, the boundaries of biogeographical regions are represented by sharp lines at certain sections and broad transitional zones elsewhere (Oliviero et al. 2013).

There is another problem in the area south of the transitional zone. In Slovenia, Wraber (1969) circumscribed a sub-Pannonian area, but he did not demonstrate the occurrence of Pannonian communities within it. Fukarek (1977, 1979), who studied the boundaries of the entire Illyrian floristic province, went even further than Wraber and declared the area between the Sava river and the northeastern flanks of the Dinaric Alps where he proposed the boundary, and also the area on the left bank of the river, as parts of the Pannonicum floristic province. Marinček (1995) placed the boundary of the Illyrian floristic province farther north, but he also considered the area north of the Sava river as part of the Pannonian floristic region. He did not support his view with evidence of Pannonian communities occurring in the long Croatian part of the area between the Drava and Sava rivers. It is clear that the aforementioned researchers relativized the Pannonian character, and did not adopt the principle that every region has to be evaluated according to its own criteria. Unfortunately, they applied both floristic and vegetation geographical arguments when establishing boundaries, which makes the repeatability of the delimitation methodology more difficult.

We argue that botanists have to accept the notion that there exist uncharacteristic areas, which are difficult or even impossible to assign to any phytogeographical region. Such an area is found between the Drava and Sava rivers, which is, in our opinion, not a part of the Pannonian vegetation region.

Coincidence of the floristic and vegetation region boundaries

We found that the boundaries of the Pannonicum floristic province and the Pannonian vegetation region did not fully coincide. The degree of deviation varies greatly. In cases when there is a rather uniform environmental gradient that is not disrupted by other environmental factors, this deviation tends to be small. This is the case in the north, where the boundary of the Pannonian flora province towards the Carpathians has been long studied (e.g., Moesz 1911, and with more species: Futák 1966). The line proposed by Futák (1966) is in good agreement with the boundary of the Pannonian vegetation region (which we determined by using mainly the map of Michalko et al. 1984–1986). The close correspondence (exceptions being only the Slovenský Kras) may be the consequence of the rather uniform altitudinal gradient to the Carpathians, which renders the boundary between the *Quercetum petraeae-cerridis* and *Carpinus betulus*-dominated forests relatively unequivocal.

In other cases, however, the discrepancy between the boundary lines of the Pannonic floristic province and the Pannonian vegetation region seems to be larger. In Western Hungary, the distance between the two lines may reach 10-60 km (Fig. 1.) This area is covered by the floristic sector of Western Dunántúl (Gáyer 1925, Jávorka 1924-25, Soó 1933, Kárpáti 1958, 1960; see the maps in Pócs 1981). The vegetation of the area has been characterized above. It essentially lacks climatically zonal Pannonian communities with the exceptions of some fragments (mostly extrazonal *Quercetum petraeae-cerridis* stands (Szmorad 1994, Király et al. 1999), and some xerothermic vegetation at the western border (Kőszeg) of the area (Gáyer 1925). Pannonian endemisms are rare here (0-1 species/cca. 140 km^2 mapping-grid units as opposed to 3-10(15) species/grid units in the middle of the basin (Bartha et al. 2015). Meusel et al. (1965) do not regard this area as part of the Pannonicum floristic province. Based on the analysis of the patterns of the Central European flora they define a region called Praenorico-Slowenian floristic subprovince, covering West- and South-West Hungary, Burgenland, South Styria and northern Slovenia. This subprovince is separated from the great provinces of Alpicum, Illyricum and Pannonicum. The subprovince has an intermediate, transitional flora. Its Eastern border is very close to the corresponding borderline of the Pannonian vegetation region. The exact method of delimitation was not published. We suggest to re-think the Western border of the Pannonicum floristic region based on the distribution of Pannonian, continental, pontic, pontic-submediterranean and xerophilous submediterranean taxa. Our expectation is that a new, alternative floristic border could be drawn closer to our vegetation region border than the floristic border delimited by Soó (1947) and Pócs (1981) (Fig. 1). Large disagreements between boundary lines exist in the east as well. In our opinion, the boundaries of the Pannonicum floristic province should be revised in the near future based on statistical analyses using modern, integrated floristic databases.

Conclusions

Methodologically, the application of high resolution maps – especially those with a scale of 1:500,000 and even of 1:200,000 – significantly modified the preliminary boundaries drawn up on the 1: 25,000,000 base map. Meticulous evaluation of the large number of vegetation descriptions, texts and data tables, helped us assess patches along the boundaries, and often led to the correction of the base map. Without this

process, the eastern boundary of the region could not have been drawn up at all.

Our method is simple, open to improvements, and the results can be validated and falsified. The small number of relevant vegetation units (in the order of ten) greatly simplifies the method compared to regionalization on a floristical basis. In this case, the regional distribution of many more units should be considered including the Eurasian (mainly South-Eurasian), continental, Pontic, Pontic-Pannonian floristic elements, Pannonian endemics, and a substantial portion of species with sub-Mediterranean distribution range (several hundred taxa, see Pócs 1981).

No doubt that maps with boundaries of phytogeographical units determined by the geographical ranges of taxa, and their gradient-like interpretations may provide answers to a number of more sophisticated questions. However, floristic data bases that are necessary to determine the boundaries are still unavailable along the eastern and southern borders.

Comparisons of boundaries of vegetation and floristic regions are rarely done. We argue that vegetation region boundaries can assist us to reevaluate long-established floristic region boundaries. We showed, however, that in some cases neighboring regions are not in direct contact: there exist uncharacteristic areas, which are difficult or even impossible to assign to any phytogeographical region.

Our map provides an opportunity to the European Union to use a scientifically more sound biogeographical circumscription of the Pannonian region in her Natura 2000 and other programs.

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Electronic Appendix

GIS file of the boundary line of the Pannonian vegetation region. The file may be downloaded from www.akademiai.com.