

Spatial modelling-based approach to phytogeographical regionalization using grassland vegetation data

Research Article

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Abstract: We presented a methodology for drawing continuous boundaries in the landscape differentiating between regions with different floristic composition. A region in Central Slovakia covering 2,445 km² was investigated. Ecological indicator values for temperature (EIT) in 1,978 grassland polygons were analysed. Ordinary kriging was used to interpolate EIT across the study region. Lattice wombling was used to identify the most intensive gradients in EIT and to draw boundaries, while ANOVA was used for post-classification analysis. A strong pattern of spatial continuity was present in EIT assigned to species in grassland polygons allowing for drawing continuous boundaries in the landscape. The study region was divided into 15 districts using the proposed method. Post-classification analysis indicated that 17 out of 23 adjacent districts were found to differ significantly in term of mean value of source samples. The results implied the need for incorporating spatial autocorrelation in sample data into post-classification analysis; such factor is often neglected in ecological research. The presented findings suggested broader applicability of the proposed method for spatial modelling, as vegetation data is widely accessible in databases for many regions of Europe.

Keywords: Ellenberg indicator values • Grassland vegetation • Phytogeographical boundaries • Spatial interpolation • Analysis of variance

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1. Introduction

The study of boundaries contributes to understanding species–environment relationships by investigating species' and communities' distributional limits [1–4] as well as the effect of changing environmental conditions on those limits [5–8]. Ecological boundaries influence the structure and functions of landscapes, and their dynamics influence diverse populations, communities, and ecosystems by way of feedback effects [9]. Two main approaches in the research of ecological boundaries focus on those boundaries' structural properties (pattern-based approach) and associated processes (process-based approach). Recently, relationships between patterns and processes have also been increasingly recognized [10–13]. Risser

[14] divided ecological boundaries into two categories – those caused by a steep gradient in environmental variables, and those caused by a threshold or nonlinear response to gradual environmental gradients. The latter are also known as metastable boundaries [9,15].

Strayer *et al.* [16] proposed the classification of boundaries on the basis of four main traits: origin and maintenance, spatial structure, functions, and temporal dynamics. On the basis of structural properties, we can distinguish between open or closed, straight or sinuous, crisp (sharp) or gradual (fuzzy) boundaries. The latter is a case of a phytogeographical boundary, as it reflects the natural variation of biota and thus forms rather broad ecotones with various types of non-equilibrium population dynamics (e.g. source-sink) [for further detail, see 17,18]. Fuzzy logic [19] has recently become an

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important concept in geosciences [20–24], and it may be used effectively for drawing ecotone-type boundaries. It enables consideration of uncertainty resulting from insufficient data and model deficiencies as well as uncertainty resulting from environmental processes that are indefinable and indeterminable [25].

The character of the underlying data is an important criterion indicating a proper method to select for boundaries delineation. These may be point *versus* grid data, regularly *versus* irregularly distributed, abundance *versus* presence-absence, *etc.* [26]. Edge detectors, lattice wombling, scale-space filters, and moment measures [4] are appropriate tools in the case of grid data. Fagan *et al.* [9] stated that tools for boundary detection on quantitative contiguous grid data include spatial clustering, fuzzy logic, kernel approaches, lattice wombling, and wavelet analysis.

Post-classification analysis is an important part of regionalization. Randomization procedures are frequently used to determine whether the identified boundaries differ significantly from boundaries produced by randomizing the data [9,26]. Emphasis may also be placed on differences between proposed regions, in terms of mean values or other statistics. Analysis of variance (ANOVA) and its variants that enable taking into account spatial autocorrelation, often present in ecological data, is suggested for this purpose [27–30].

The method proposed in this paper uses Ellenberg indicator values for temperature (EIT) assigned to taxa in a floristic grassland database. Despite many objections [e.g. 31–36], Ellenberg indicator values are widely used in botany and plant ecology [37]. Compared to physical and chemical measurements, indicator systems circumvent measuring those resource fractions actually accessible to plants and integrate across the spatial and temporal variability of sites [38]. The use of various

cover-weighting schemes to calculate the average indicator value of vegetation relevés is common practice in ecological studies [39–41]. Recently, this concept has been thoroughly discussed by Käfer and Witte [42].

This paper strives to propose a methodology for definition of boundaries in the landscape that differentiate between regions with significantly different plant composition. We hypothesize that widely available floristic databases contain sufficient information for drawing such boundaries. We expect that EIT assigned to species in grassland polygons exhibit a sufficient pattern of spatial continuity to allow for drawing continuous boundaries. Such method is applicable, for example, in a broader surrounding of intra-Carpathians basins with intensive climatic gradients and mosaic occurrence of semi-natural grasslands, as presented in this study. In particular, we focused on (i) identification of a series of phytogeographical districts using grassland vegetation data in Central Slovakia, (ii) assessment of statistical significance of differences in EIT between the adjacent districts (post-classification analysis), and (iii) discussion of broader applicability and limits of such approach for phytogeographical regionalization. The presented results complement the work of Turisová and Hlásny [43].

2. Experimental Procedures

2.1 Data

A region in Central Slovakia (Central Europe) spanning 2,445 km² was investigated (Figure 1). Morphologic diversity (mountains *vs.* basins) is enhanced by the complex geological setting as well as by a broad spectrum of floristic taxa. Elevation ranges from 223 to 1,750 m a.s.l. Mean annual air temperature ranges

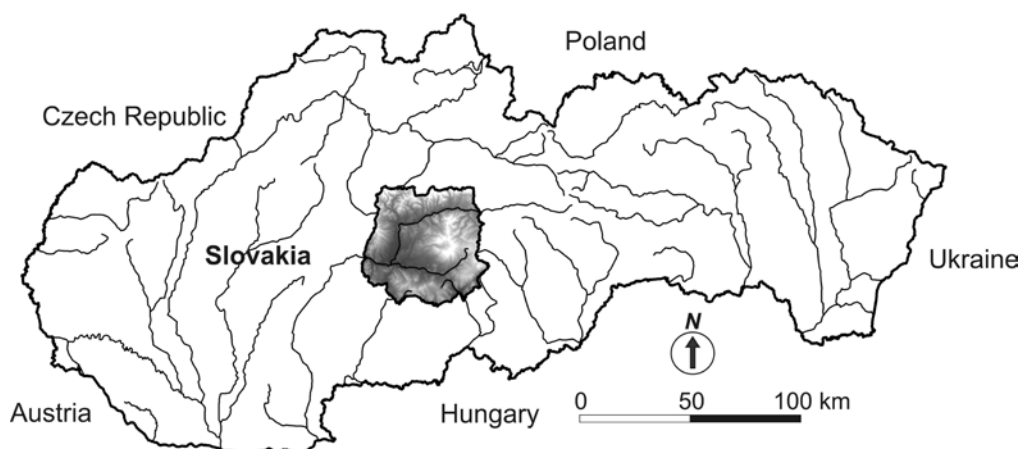


Figure 1. Position of the study region. Generalized river network of Slovakia is presented.

between 7.7°C and 8°C, while air temperature during the vegetation season (IV–IX) ranges between 10.9°C and 14.4°C. Annual precipitation ranges between 610 and 797 mm (average data for the last 30-year period are presented). The units ranging from *Potentillo albae-Quercion* to *Eu-Fagenion* p.p.maj. represent the region's potential vegetation. At present, agricultural land combined with fragments of grasslands (dominated by *Festucion valesiacae*, *Bromion erecti*, *Arrhenatherion elatioris* and *Cynosurion cristati*) occur in valleys. Higher elevations feature mostly secondary forests dominated by spruce (*Picea abies*), mountain meadows and pastures (*Polygono bistortae-Trisetion flavescens*, *Violion caninae*, *Nardo strictae-Agrostion tenuis*).

The data (taxa of vascular plants) was gathered within the cluster of projects focused on the establishment of the NATURA 2000 network in Slovakia. All grasslands were identified using aerial imagery and subsequently mapped in the field by 22 surveyors during 1995–2005. Only semi-natural grasslands, not intensified and overgrown by trees and shrubs, were mapped. All taxa and their coverage on the Tansley scale [44] were recorded. Mapping methodology is described by Šeffer *et al.* [45].

EIT were assigned to species records using the JUICE 7.0 program [46]. Taxa recorded in the region take on EIT in a range of 1–8, which indicates species transition from thermophilous to psychrophilous. Indicator values have been assigned to 71% of determined taxa. Indicator values could not be assigned to infraspecific taxa (9%), taxa determined by tribe and genus (15%), Carpathian (sub)endemic species (3%), and (sub)Pannonian species (2%).

To facilitate geostatistical analysis, the arithmetic average of EIT in each polygon was assigned to the polygon's centre point. As the mapping methodology implies that polygons are homogenous at the level of alliance and sub-alliance, and given that each polygon comprises 60 to 140 species, this number of species appears sufficient to provide an unbiased estimate for the mean value of EIT within polygons. Although species coverage was recorded on the Tansley scale

(1 – <1%, 2 – 1–50%, 3 – 50–100%), we decided not to use a cover-weighted average of EIT, as such approach could allocate large weights to species that easily reach high abundance while solitarily growing and strongly indicative species could be underweighted [41]. In fact, differences in basic statistics between the outputs obtained using the cover-weighted approach *versus* the unweighted approach were minor. Table 1 presents descriptive statistics of the data used.

2.2 Methods

The proposed methodology consists of spatial interpolation of EIT assigned to grassland polygons (as described above) throughout the study region using ordinary kriging. To draw a border, it is assumed that the steepest gradient in EIT between adjacent grid cells indicates the most radical changes in floristic composition, typical of border locations [47]. This method is also referred to as lattice wombling [9,26,48]. The relevance of the generated division was evaluated using adjusted ANOVA accounting for spatial autocorrelation [30].

A variogram is a geostatistical tool for investigating the spatial dependence (autocorrelation) of various phenomena [for detail, see 49–51]. Variograms are used in two ways in this study – as an input to ordinary kriging, and as an input to ANOVA to account for spatial autocorrelation in the investigated data (described in greater detail below).

Ordinary kriging is a stationary univariate technique for spatial interpolation, *i.e.* it provides estimates for unrecorded locations on the basis of measured samples. The spatial correlation between source data (expressed in terms of a variogram or covariance function) is a part of the kriging system.

Wombling is a general method for identifying zones of abrupt change, and is named after Womble (1951), the author of the seminal article on the subject. This method has several forms, depending on the nature of the data (point referenced, areal, lattice, or transect). In addition, algorithms differ depending on whether categorical or numerical data are processed, or whether fuzzy or crisp boundaries are defined. It is a kernel-based technique, *i.e.* a kernel of specified size passes through the sampling and computes rates of change among neighbouring sampling units. These can be calculated as absolute differences, first or second partial derivatives of each of four quadrates forming a square [52]. While the first-order derivative indicates a boundary position, the second-order derivative identifies the inflection points where a boundary ends [53]. A boundary is identified by spatially adjacent locations characterized by high values of the rate of change. A more detailed description is given by Bocquet-Appel

Number of grassland polygons	2,092
Number of valid taxa records	116,180
Number of taxa records with assigned Ellenberg indicator values of temperature	56,134
Number of valid taxa	1,071
Number of taxa with assigned Ellenberg indicator values for temperature	736

Table 1. Source data description.

and Bacro [54], Fagan *et al.* [9] and Lu and Carlin [55].

ANOVA with autocorrelated data determines whether the identified units of spatial division are significantly different in terms of mean values of sample data. The problem implies using standard one-way ANOVA. However, spatial autocorrelation in source data disrupts standard tests of significance. This problem has long been discussed as it is common in many fields of research [27–29]. Positive autocorrelation causes differences between groups that are not truly different to be declared significant. Negative autocorrelation acts in the opposite manner. SAS PROC MIXED (version 8; <http://support.sas.com>) allows for using several variogram models to describe the positive spatial autocorrelation in analysed data, and thus to modify the ANOVA to account for spatial autocorrelation in sample data. Hong *et al.* [30] documented use of this technique on agricultural data. The authors also provided the program code which was used to run such analysis in this paper.

3. Results

The variogram of EIT assigned to grassland polygons indicates that such data are spatially highly continuous and that spatial dependence between data disappears beyond a distance of 12 km. Two structures were used to fit the empirical values – a nugget effect component (discontinuity at variogram origin due to small-scale variability in the data) and isotropic spherical variogram

(Figure 2). Such variogram was used in spatial interpolation using ordinary kriging. The resulting map is presented in Figure 3a.

GIS techniques were used to calculate the gradients in the generated surface of EIT (Figure 3b). The boundaries were drawn by hand through local maximums of gradients, forming the ridgelines. The study region was divided in this way into 15 districts (Figure 4, Table 2).

The proposed districts were analysed to ascertain whether they differ significantly in terms of mean values of EIT of source samples. The analysis aims

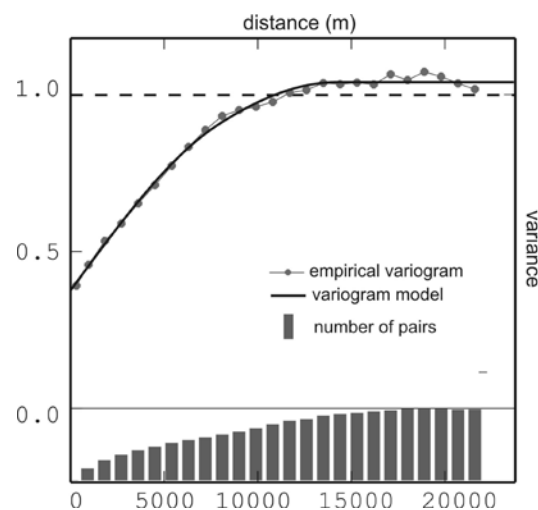


Figure 2. Isotropic variogram of Ellenberg indicator values for temperature assigned to grassland polygons.

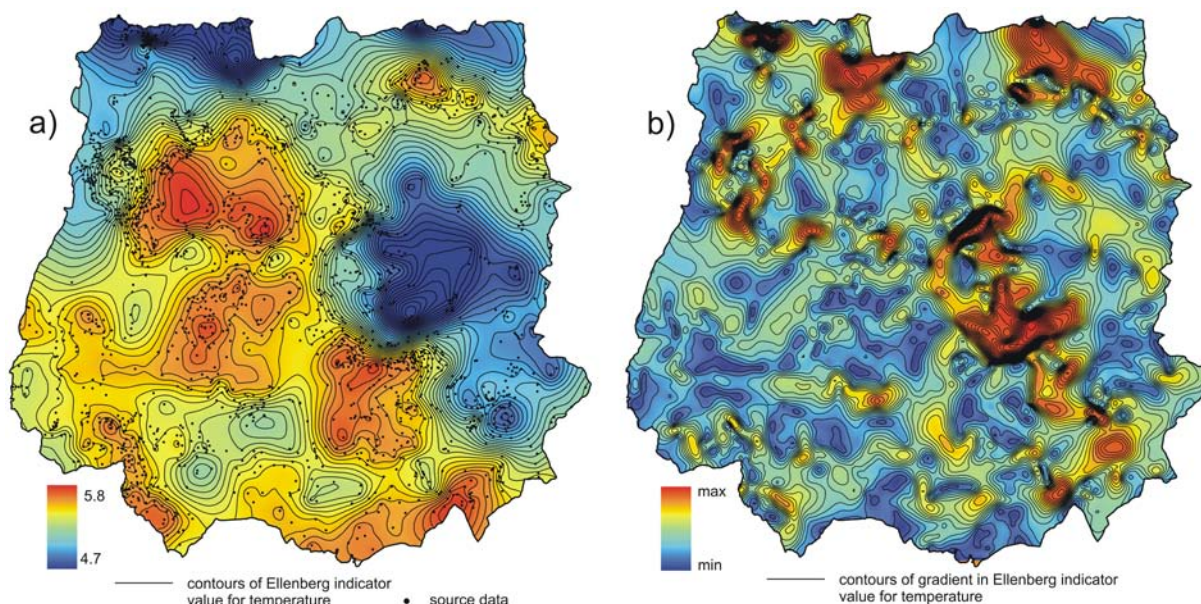


Figure 3. Map of Ellenberg indicator values for temperature produced using spatial interpolation of indicator values assigned to grassland vegetation polygons (a), and gradients calculated from the map thereof used to designate the boundaries between districts with different floristic composition (b). Respective isolines are displayed.

District	N	Mean	Median	Min	Max	St. dev.
C1	87	5.054	5.077	4.429	5.432	0.191
C2	122	5.239	5.263	4.719	5.810	0.148
C3	139	5.322	5.347	4.231	5.656	0.195
T1	52	5.303	5.308	4.818	5.658	0.193
T2	264	5.473	5.500	3.000	6.067	0.295
T3	113	5.506	5.500	5.150	5.854	0.138
T4	105	5.501	5.500	5.000	5.818	0.132
T5	32	5.411	5.353	5.000	6.000	0.224
W1	286	5.710	5.722	5.167	6.174	0.151
W2	210	5.673	5.667	5.171	6.162	0.177
W3	431	5.626	5.622	5.100	6.136	0.159
W4	90	5.689	5.677	5.333	6.059	0.170

Table 2. Descriptive statistics of source samples (Ellenberg indicator values for temperature assigned to taxa in grassland polygons) in 12 districts with floristic composition differing in species demands on temperature.

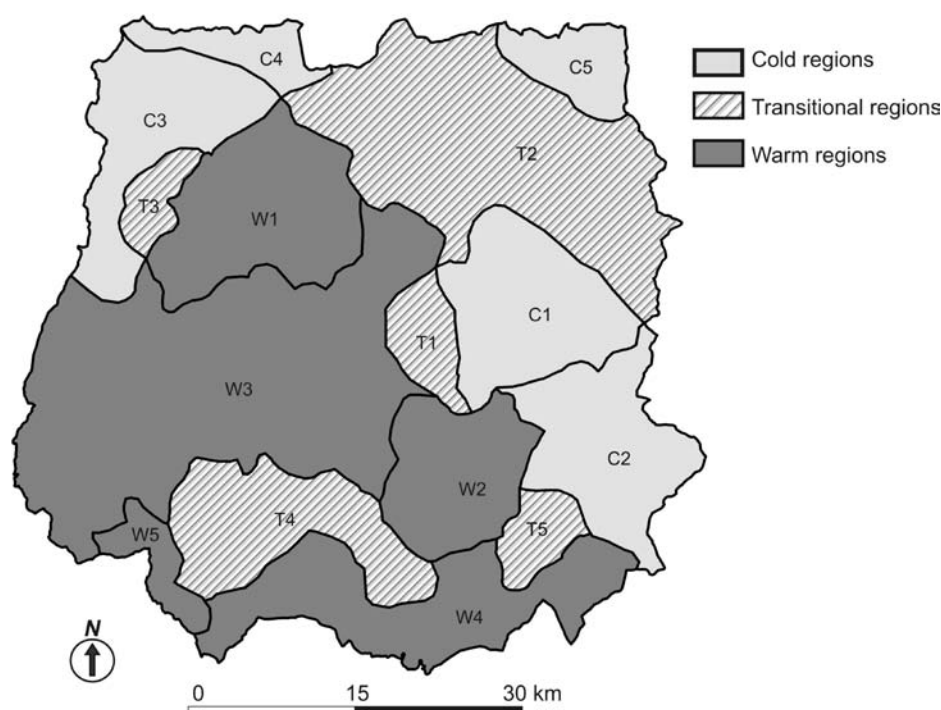


Figure 4. The proposed division of the study region into 15 districts with floristic composition differing in species demands on temperature.

at adjacent districts only, and thus 23 tests have been conducted in total. An isotropic variogram was constructed for each couple of adjacent units to reduce the number of degrees of freedom proportionally to the spatial autocorrelation of sample data when using the modified ANOVA.

Only 12 out of 15 designated units were analysed (Table 3). Units C4, C5 and W5 are only minor parts

of more spacious units stretching into the study region from the outside.

The adjusted ANOVA test revealed that the mean values of 17 out of 23 adjacent subdistricts differed significantly at 99% significance level. Another couple of districts were found to differ at 95% significance level.

To investigate the effect of spatial autocorrelation on performed tests, we provide a comparison of

	C1	C2	C3	T1	T2	T3	T4	T5	W1	W2	W3	W4
C1	X	-	-	-	-	-	-	-	-	-	-	-
C2	0.921	X	-	-	-	-	-	-	-	-	-	-
	0.000**											
C3	-	-	X	-	-	-	-	-	-	-	-	-
T1	0.000**	-	-	X	-	-	-	-	-	-	-	-
	0.000**											
T2	0.175	-	-	-	X	-	-	-	-	-	-	-
	0.000**											
T3	-	-	0.201	-	-	X	-	-	-	-	-	-
	0.000**											
T4	-	-	-	-	-	-	X	-	-	-	-	-
T5	-	0.799	-	-	-	-	-	X	-	-	-	-
	0.000**											
W1	-	-	0.900	-	0.000**	0.001**	-	-	X	-	-	-
			0.000**		0.000**	0.000**						
W2	0.000**	0.000**	-	0.000**	-	-	0.113	0.000**	-	X	-	-
	0.000**	0.000**		0.000**			0.000**	0.000**				
W3	-	-	0.000**	0.000**	0.000**	-	0.008**	-	0.000**	0.011*	X	-
			0.000**	0.000**	0.000**		0.000**		0.000**	0.001**	-	-
W4	-	0.000**	-	-	-	-	0.628	0.074	-	0.660	-	X
	0.000**					0.000**	0.000**	0.452				

Table 3. Post-classification analysis. Statistical significance of differences in mean values of source data between adjacent districts is investigated. X denotes the diagonal cells. The upper number denotes p-value produced using ANOVA adjusted for spatial autocorrelation, the lower number denotes p-value produced using standard ANOVA (** 99% significance level, * 95% significance level).

p-values produced by both standard and adjusted ANOVA (Table 3). It is apparent that adjusted ANOVA (accounting for spatial autocorrelation in source data) is a stricter test as compared with standard ANOVA. In total, the null hypothesis of no difference in mean values of source samples between adjacent subdistricts was rejected in 22 out of 23 tests performed using standard ANOVA, while the null hypotheses was rejected in only 17 tests performed using adjusted ANOVA (99% significance level).

4. Discussion

In view of recently developed floristic and vegetation databases, it is a timely task to develop a data-driven approach to phytogeographical regionalization using such databases. We have proposed an approach based on the spatial modelling of Ellenberg indicator values and floristic data and demonstrated its use in a model region using records on floristic composition of grasslands.

We found that the species records in the database contained sufficient information to draw continuous boundaries in the landscape, or, more specifically, that there is a strong pattern of spatial continuity in

Ellenberg indicator values assigned to species data and averaged in grassland polygons. As such database is publicly available and has national coverage, this finding allows for proposing a phytogeographical regionalization for all of Slovakia. Databases with similar content and national coverage (especially national vegetation databases) are available for many regions of Europe as well [56], and hence the proposed methodology, or variants thereof, can be thought of as widely applicable. Both floristic and vegetation databases can be used and/or combined using the system of ecological indicators. Wamelink *et al.* [57] suggest, however, that Ellenberg indicator values should not be combined between various vegetation types. The aforementioned combination of vegetation and floristic databases on the basis of ecological indicators should therefore be treated with care. The use of large databases also raises a question as to the effect of species which could not be assigned an indicator value or, more generally, as to the effect of the completeness of vegetation relevés. In the present study, 29% of all species determined could not be assigned an EIT. Ewald [58] suggests in this regard that the correlation of Ellenberg indicator values with environmental measurements is only weakly affected by leaving out low-abundance species. In the case of

temperature, the R^2 decreased from 0.53 (full species matrix) to 0.37 when only 20% of the original species list remained. Finally, the author suggests that Ellenberg indicators can be thought of as relatively resilient to incomplete sampling.

The other critical finding is the need to take into account the spatial autocorrelation in the post-classification analysis. This fact is often neglected in ecological studies. Positive autocorrelation causes differences between groups that are not truly different to be declared significant. This was the case in 7 out of 23 tests performed. Such tests provide complementary information indicating the relevance (reliability) of proposed regionalization. Some boundaries drawn on the basis of gradients on the surface interpolated from ecological indicator values can be re-evaluated if no significant differences were found between the adjacent districts in terms of mean values of source samples.

Another question is whether the identified districts and subdistricts differ from each other in terms of characteristic and/or diagnostic species. Turisová and Hlásny [43] found, in a related study, that most designated districts were well separated in terms of the presence of a certain number of diagnostic species in each district. This lends support to the applicability of the proposed approach for designating regions with specific species composition.

Boundaries' scale dependence was not discussed in this paper, although it is an integral concept of regionalization [56,59]. In this regard, Cadenasso *et al.* [13] stated that scientists must choose their grain size deliberately and specify it in their publications. However, the scale of delineated borders in this article is determined mainly by the structure of the surface produced by kriging. Therefore, not grain size but rather the range of the underlying variogram is a proper indicator of scale.

In this study, we focused our attention on ecological indicators of temperature, although other indicators (moisture, nutrients, light, continentality, soiltype, *etc.*)

are also viable for phytogeographical regionalization [60-62]. Their use depends mainly on the leading processes that control vegetation distribution in a given region. Regionalization based on multiple indicators can be performed as well. Multivariate geostatistical techniques facilitate the combination of multiple factors in a straightforward manner using the method proposed in this paper.

Unevenly distributed source data also raise a question with regard to the reliability of the boundaries generated, particularly at under-sampled locations. There are several aspects to this issue, for example: Does the boundary differ significantly from a boundary produced by randomizing the data? Do selected statistics differ significantly between neighbouring units? Does the uncertainty associated to a boundary segment/single location exceed some threshold? Randomization procedures [9,26] and testing differences of mean values between neighbouring regions [27-29], as seen in this paper, are two possible methods. With regard to the geostatistical background of the proposed methodology, kriging variance [63], calculated along with kriging estimates, may be a proper measure to determine boundary uncertainty arising due to prediction errors. Conditional simulations [64,65] are an effective option as well

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