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Complex analysis of spatial vegetation gradients and boundaries on the example of the Villány Mts and Mt Tubes

PhD Thesis

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1. INTRODUCTION

The research of ecological gradients and boundaries is important both from a theoretical and a practical point of view. Arrangement of communities and populations along gradients may provide us with basic information about functioning of supraindividual organization levels. The concept of within-patch and between-patch gradients in vegetation ecology can serve as a general frame for future researches.

Boundaries are space-segments where gradients are steeper than elsewhere. Boundaries are important because they separate communities from each other. Although the area occupied by boundaries may be relatively small, they role is extremely important, because they control the ecological flows. Landscapes consist of patches corridors and boundaries, thus knowledge on boundaries in indispensable in landscape ecology. Boundaryes may play an important role in nature conservation as well: due to habitat fragmentation, proportion of boundaries is increasing, and responses of boundaries to global changes also need to be understood.

In my dissertation I focus on vegetation gradients and boundaries. I make an attempt to define terms related to gradients and boundaries; I try to contribute to the better knowledge on the properties of the moving split window analysis (MSW), based on simulated gradients; and I carry out a complex analysis of vegetation gradients of southern Transdanubian mountains.

2. QUESTIONS AND AIMS OF THE STUDY

1.) Proposal for a unified terminology on ecological gradients and boundaries
2.) Contribution to the knowledge on the moving split window analysis (MSW), using simulated gradients
- Which kind on randomization is appropriate in MSW-analyses?
- Can transitional and non-transitional zones be distinguished by the MSW-method?
- Is MSW able to indicate distinctness of transitional zones?
- How is it possible to distinguish between boundaries of different scales with the MSW-method?
3.) Arrangement of communities, based on vegetation profiles
- What is the order of plant communities along the gradients under study?

4.) Detectability of community boundaries
- Are visually detected and MSW-detected boundaries in the same position?
- What information can be gained by comparing possible differences between the results of visual detection and MSW-detection?
5.) Comparison of north-facing and south-facing mountain slopes
What is the difference between the vegetation of differently exposed slopes, concerning the above characteristics:
- number of community boundaries,
- number of population patches,
- size of population patches,
- species richness?
6.) Boundaries of different scales
- Are there boundaries of different scales along the gradients under study?
7.) Transition between the mesic and xeric community complexes
- Where is the transition between mesic communities of the north-facing slopes and xeric communities of the south-facing slopes?
- On the study scales, should this mesic-xeric transitional zone be regarded as a boundary zone or as a boundary line?
- What kind of species groups are typical in the transitional zone?
- Is the species composition of the transitional zone distinct from the mesic and xeric community complexes?

3. MATERIALS AND METHODS

3.1. Study area

For field studies, three parts of the Villány Mts (Mt Fekete, Mt Szársomlyó, Mt Tenkes) and one part of the Mecsek Mts (Mt Tubes) were chosen. Vegetation of these mountains is near-natural and their plant communities are well-known. From the north-facing slopes to the south-facing ones, the existence of a complex environmental gradient can be supposed. Several plant communities can be found along this gradient. North-facing slopes are covered mostly by mesic forests, while there are xeric grasslands and forests on the southern slopes. It can be presumed that boundaries of different sharpness may exist between the different communities. Further, it can be assumed that boundaries of at least two different scales should be present in the study area: fine-scaled community boundaries and coarse-scaled boundaries between the differently exposed slopes.

3.2. Field works

Vegetation profiles were made from the northern foot of the mountains to the southern foot in the case of Mt Fekete, Mt Szársomlyó and Mt Tenkes.

In addition, six intensive transects were established (five in the Villány Mts and one on Mt Tubes). Transects were perpendicular to the mountain ridges, their length was 200 m (Villány Mts) or 382 m (Mt Tubes). Each transect consisted of 1 m² contiguous plots. Relevés were made in each plot in April and in July, estimating percentage cover of all vascular plant species.

3.3. Preparation of artificial data matrices

Seven datasets were used, representing seven possible species distribution patterns. The first dataset consists of three distinct communities along a gradient, with no species overlaps. In the second dataset, central community is a transitional one, possessing its own species as well. In the third dataset, boundaries are blurred, and the central patch does not have its own species. Species number is higher in the central patch than in the other sections. In the fourth dataset, the boundaries between the communities are blurred, and the species number is roughly the same along the whole gradient. (It should be noted that distinctness of the central patch is decreasing from the first to the fourth dataset.) In the fifth dataset, the central patch is a habitat patch situated in a homogeneous matrix.

In the sixth data matrix, the gradient was split into two sections with different species composition. Both sections were divided into small patches, thus the gradient consits of two neighbouring mosaic complexes. The seventh data matrix is similar to the sixth one, but here, there is a continuous change of species composition in the first part of the gradient. (It should be noted that there are boundaries of two different scales in the case of the sixth and seventh data matrices.)

3.4. Moving split window analysis

Both simulated gradients and field data were analysed with the MSW-method. As comparative function squared Euclidean distance was applied. Z-score transformation was used to test the significance of the boundaries. To compare randomization procedures, three randomization types were applied: complete randomization, plot randomization, random shift. The overall mean and standard deviation were computed from 99 randomizations in all cases. Z-scores were computed for all window widths between 2 and 60, and values were plotted against window midpoint position. As random shift proved to be the most useful method, only this randomization was used thereafter. In all other MSW analyses, z-scores were averaged as follows. In the case of the simulated data matrices, z-scores were averaged over 10-20, 30-40 and 50-60 window widths. In the analyses concerning boundary detectability and sharpness, as well as in the analyses on differences between north-facing and-south-facing slopes, averages 2-20 were used. When investigating the mesic-xeric transition and the boundaries of different scales, z-scores were averaged over 10-20, 30-40 and 50-60 (in the case of Mt Tubes, 70-80 as well) window widths.

3.5. Other analyses

Intensive transects were analysed using PCoA-ordination. As comparative function, Jaccard index was used.

Transects were split into a north-facing and a south-facing segment. Number and size of the population patches were determined for the contrasting segments. To investigate the effect of exposure on the patch sizes, three generalized linear models were built. Model selection was done based on AIC-values. In the case of Mt Tubes, located farther away, Mann-Whitney U-test was applied for comparison.

In the case of three transects, transects were split into three segments, according to the z-score profile: transitional zone was located between double peaks of the MSW. The mesic part was north of the transitional zone, and the xeric part was south of the transitional zone. Withis each segment, spectra of the ecological indicator values were computed. Differential species of the three segments were identified, and finally, coenological preference of the differential species was examined.

4. RESULTS AND DISCUSSION

4.1. Proposals for the terminology

I gave proposals concerning the definitions of the terms related to gradients and boundaries. The *spatial boundary* is a segment of space separating and at the same time connecting two neighbouring segments of space. The two entities on both sides of the boundary must differ from each other from the point of view of the research question, and their extent has to be much wider than that of the boundary. The boundary is the locality in which the transition occurs from one side to the other. The very same boundary can appear as a *boundary line* or as a *boundary zone*, depending on the resolution. *Ecotone* and *ecocline* are spatial gradients of background factors; in the case of ecotone, the gradient is steep, while in the case of ecocline it is gradual. *Coenotone* and *coenocline* are spatial gradients of communities; in the case of coenotone, the gradient is steep, in the case of coenotone, it is gradual. *Ecotone zone* is a segment of space in that an ecotone can be found. *Ecocline zone* is a segment of space in that there is an ecocline. Similarly, *coenotone zone* and *coenocline zone* are segments of space; the former contains a coenotone, the latter a coenocline. *Transitional zone* is a segment of space containing some kind of transition (gradient). There are two contrasting types of ecological boundaries, between which several transitional types are also possible: *ecotonal boundary* and *ecoclinal boundary*. *Coenotonal boundary* (limes convergens) and *coenoclinal boundary* (limes divergens) are types of synphenobiological boundaries (in our case, vegetation boundaries) (transitional types are possible here as well). *Edge* is a synonym of boundary. An edge forms between two neighbouring patches, and is considerably narrower than those. In contrast, *edge effect* can be wider, and may cover the whole area of a smaller patch.

4.2. Properties of the MSW, based on artificial data matrices

My results indicate that shape of the z-score profile is not affected very much by the type of the randomization procedure. In contrast, randomization type can have a major influence on the height of the z-score peaks. If complete randomization or plot randomization is used, peak heights vary considerably with increases in window size. In contrast, height of peaks is almost independent of the window width in the case of random shift.

My results supported the findings of KÖRMÖCZI (2005), showing that MSW is able to distinguish true transitional zones from zones that do not have a real transitional character. If a zone does not have a transitional species composition, peaks indicating borders of the transitional zone do not merge if window widths are increased. In contrast, if a zone forms a transition between two communities along a gradient, peaks merge at larger window widths.

KÖRMÖCZI (2005) stated that coalescence of the MSW-peaks depends on the width of the transitional zone. My results emphasize that other factors should be taken into account as well: independence (i.e. distinctness) of the zone influences at which window sizes peaks merge. If the transitional zone is relatively independent (e. g. it has its own species or a greater species number than the neighbouring communities), then peaks merge only at the largest window widths. If independence of the transitional unit is lower, double peaks merge at smaller window widths.

My work has shown that MSW is able to differentiate between boundaries of different scales. However, this is only possible if multiple window sizes are used in the MSW analysis. At small window widths, boundaries of both coarser and finer scales are detectable, but boundaries of different scales are hard to separate. At large window widths, significance of peaks indicating fine-scale boundaries drops, while peaks referring to coarse-scale boundaries are highly significant. This also indicates where future field studies using MSW could be improved. Most studies use one or a few similar window widths, which does not enable the detection of boundaries of different scales.

4.3. Vegetation profiles

During my work, I prepared the vegetation profiles of Mt Fekete, Mt Szársomlyó and Mt Tenkes. On the northern slopes of Mt Szársomlyó and Mt Tenkes, oak-hornbeam forests dominate, while the northern side of Mt Fekete is covered mainly by tree plantations. In norhern exposures, top-forest stands were also identified. Near the ridges, in northern exposures, stands *of Festuco rupicolae-Arrhenatheretum* can be found. On the southern slopes, shrubforest-rock sward mosaics and vergilius oak forest-slope steppe mosaics are typical. Hillfoots are usually covered by vineyards.

If vegetation profiles of the Villány Mts are compared to those of Mt Tubes (Mecsek Mts), following differences can be seen (cf. MORSCHHAUSER 1995; KEVEY and BORHIDI 1998): on Mt Tubes, beech forests play a more important role, *Festuco rupicolae-Arrhenatheretum* is lacking, and there are less shrubforests and rock swards on the southern slope, but greater areas are occupied by vergilius oak forests. Besides, the extent, position and role of top-forests differs considerably. In the Mecsek Mts, top-forests occupy wide zones on mountain tops and on the higher parts of the north-facing slopes. In contrast, top-forests of the Villány Mts are confined to a narrow zone of the steep northern slopes, near the ridges. These differences can be explained by different habitat conditions and different land-use history. The ridges of the Villány Mts are sharper than on Mt Tubes, therefore the plateau-region, the ideal habitat of the top-forests (KEVEY 2008; KEVEY és BORHIDI 2010) is lacking or narrow. In addition, areas near the ridge in the Villány Mts are rocky and stony, preventing the establishment of closed forests. Last but not least, grazing activity in the Villány Mts affected areas near the ridges, thus top-forests could survive only farther away from the ridges, where there was no grazing (on Mt Tubes, grazing was abandoned much earlier).

4.4. Community boundaries along the transects

During field studies, several boundaries between the mesic communities of the northern slopes were delineated, but these boundaries were not detected by the MSW. The explanation of this is that communities often intergrade continuously on the northern slopes. On the other hand, during field studies, boundary delineation was done based on all vegetation layers. Since field layer of the mesic communities is quite similar, in pratice, boundaries were often drawn based on the shrub or canopy layers. In sum, field layer changes gradually on the northern slopes, whereas shrub and canopy layers change more abruptly. Field layer of mesic forests showed gradual transition (without sharp boundaries) in the study of PENKSZA et al. (1995), using much larger quadrats.

It can be supposed that different background factors control the field layer and the other layers. The most important factor controlling the shrub and the canopy layers is probably thickness of the soil. In contrast, light could be the most important environmental factor for the field layer. This may be an explanation of the fact that sharp boundaries have been found where mesic forests adjoin a closed rock sward or a shrubforest with an open canopy.

On the southern slopes, visually observed boundaries of all vegetation layers coincide with MSW-detected boundaries of the field layer, because changes in soil depth coincide with changes in canopy cover.

Based on the species distribution patterns along the transects, the z-score profiles of the MSW and the population level studies, it seems that field layer communities of the mesic north-exposed slopes change continuously into one another (this can be considered a coenocline), while there are sharp (coenotonal) boundaries between the field layer communities of the xeric south-exposed slopes.

My results emphasize that one must be careful when evaluating MSW profiles. First, MSW revealed some boundaries within communities. These refer to internal heterogeneities, and should not be considered community-boundaries. Second, some almost-significant boundaries coincide with visually observed boundaries. These z-score peaks should be considered potential boundaries

4.5. Differences between north-facing and south-facing slopes

I found considerable differences between south-facing and north-facing slopes in the Villány Mts and on Mt Tubes. Plant communities show a clear preference either towards the northern or towards the southern slopes. Moreover, southern slopes can be characterized by a patchier pattern on both the population and the community level: there are more community boundaries in the field layer of the southern slopes, where population patches are smaller in diameter but greater in number. This supports the hypothesis of JAKUCS (1972), who claimed that under sub-Mediterranean and sub-Continental climates, southern slopes are more patchy than northern ones. Furthermore, my results show that communities of the field layer are richer in species on the southern slopes than on the northern ones.

4.6. Boundaries of different scales

Along the transects in the Villány Mts and on Mt Tubes, I managed to identify boundaries of two different scales. Boundaries of the finer scale can be found between xeric communities on the southern slope, while boundaries of the coarser scale have formed between the xeric and the mesic community-complexes. Spatial position of the coarse-scale boundary is not the same in the two mountain areas: in the Villány Mts, it can be found mostly slightly north of the ridge, while on Mt Tubes it is somewhat south of the plateau.

According to VAN DER MAAREL (1976), fine-scale boundaries along my transects are phytocoenose boundaries, and the coarse-scale boundary is a boundary between two phytocoenose-complexes. Using the terminology of WESTHOFF (1974), fine-scale boundaries are community-boundaries, the coarse-scale boundaries are boundaries of vegetation complexes.

4.7. Boundary between the mesic and xeric community complexes

When examining the transition between the vegetation of the north-exposed and south-exposed slopes in the Villány Mts, I found that in three of the five transects (F3, SZ2, SZ3), the community *Festuco rupicolae-Arrhenatheretum* forms the transition between the mesic and the xeric community-complexes. This unit has its own two boundaries at smaller window widths, but, at larger window widths, peaks merge. The analysis of the ecological indicator values suggests that this transitional grassland has mostly intermediate ecological properties between the mesic and the xeric complexes, but it is more similar to the xeric one.

Results differed in the case of transects SZ1 and T1. In the case of SZ1, transitional characteristics of *Festuco rupicolae-Arrhenatheretum* were less obvious. Here, this grassland is more similar to the mesic communities (probably because of the local microclimatic conditions). In the case of T1, *Festuco rupicolae-Arrhenatheretum* is more similar to the xeric communities.

On Mt Tubes (transect MT1), transition occurs on the southern slope, within a vergilius oak forest stand with a relatively open canopy layer, adjoining a rock sward. During previous studies, top-forests seemed to be transitional (KEVEY and BORHIDI 1998, 2010). The explanation for this seeming contradiction is that only the field layer was sanpled in my study. Since field layer of the top-forest is not transitional, the main change does not occur here. Studying the field layer, MORSCHHAUSER and SALAMON-ALBERT (2001) found that mesic-xeric transition occurs ont he southern slope, which is similar to my results (location of the main peak on the MSW-profile.

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