ECOLOGICAL BOUNDARIES AT DIFFERENT SCALES: TESTING THE MOVING SPLIT WINDOW ANALYSIS USING ARTIFICIAL AND FIELD DATA

ABSTRACT: Scale-dependency is one of the well-known features of ecological boundaries. Unfortunately, there are relatively few case studies analysing boundaries of different scales. Moreover, properties of moving split window (MSW) technique, a method potentially suitable for examining boundaries at several spatial scales, are not fully understood. In this study, we used artificial data sets to test the capacities and limitations of the MSW method. We also applied field data from the Mecsek Mts (Hungary) (611 m a.s.l.) in order to reveal possible boundaries at different scales and to contribute to the knowledge on vegetation pattern of mountain areas. We found that one should apply several window-widths when using MSW, since this is the only way to detect and differentiate between boundaries of different scales. Our study revealed the vegetation pattern of Mt Tubes: there is a series of continuously intergrading mesic communities on the northern slope, while the southern slope is occupied by a mosaic of different xeric communities. In this pattern, boundaries of two different scales have been identified. We conclude that MSW could effectively be used in similar mountain regions to analyse herb layer vegetation patterns and boundaries.

KEY WORDS: moving split window (MSW), gradient, transect, edge detection, simulated communities, Squared Euclidean Distance, Mecsek Mts

1. INTRODUCTION

The study of ecological boundaries is one of the most current research topics (Cadenasso et al. 2003, Yarrow and Marín 2007, Erdős et al. 2011b). An ecological boundary separates two adjacent patches: the boundary is the location where the rate of change is the highest between the two patches (Fortin et al. 2000). Boundaries are important both structurally and functionally in ecological systems (Cadenasso et al. 2003). The area occupied by boundaries is usually small, but their role is extremely important, because they control the flows of organisms, materials, energy and information (Wiens et al. 1985, Strayer et al. 2003). Ecological boundaries form a central issue in landscape ecology and nature conservation (Jagomägi et al. 1988, Ries et al. 2004).

It is well-known that ecological boundaries exist over a wide range of spatial scales and organizational levels (van der Maarel 1976, Gosz 1993, Peters et al. 2006). However, only a few studies have been carried out examining the very same field data with the very same methods at different spatial scales (e.g. Ludwig and Tongway 1995, Walker et al. 2003). There is an urgent need for more
case studies that examine boundaries at multiple scales, which would promote a better understanding of connections between different spatial scales (cf. Kolasa and Zalewski 1995, Kent et al. 1997, Laurance et al. 2001).

Objective boundary delineation is a key issue in vegetation ecology, since it may help identify the organizational rules of communities (Zalatnai 2008), examine their reaction to environmental changes (Tólgyesi and Körömöczi 2012) and protect natural values (Erdős et al. 2011a).

Several methods exist for the study of ecological boundaries (Huékens et al. 2009). Classification and ordination techniques may give useful results under some circumstances, but generally, they are not very efficient when delineating boundaries (Erdős et al. 2008). Wavelet analysis can also be used (Dale and Mah 1998), but its interpretation is rather ambiguous (Huékens et al. 2009). Wombling is a method suitable for two dimensional boundary detection (Fortin 1994, Fortin and Drapeau 1995, Fagan et al. 2003). A serious drawback of wombling is that it requires very intensive field sampling, which would result in degradation in the case of sensitive natural habitats. Among boundary analysis methods, the moving split window (MSW) is considered the best one (Kent et al. 1997), because it is relatively simple but powerful (Johnston et al. 1992). Performance of the MSW has been studied using simulated data with known properties (Brunt and Conley 1990, Körömöczi 2005). Also, MSW has been effectively used in ecological studies in several field situations (e.g. Zalatnai and Körömöczi 2004, Hennenberg et al. 2005, Zalatnai et al. 2007, Kröger et al. 2009, Erdős et al. 2011a, 2012, Xu et al. 2012). However, a great disadvantage of the MSW technique is that its capacities in analysing boundaries of different spatial scales is poorly known. There are very few publications that use the MSW with considerably differing window sizes (Ludwig and Tongway 1995, Muños-Reinoso 2001, 2009), while most case studies use one single (or a few very similar) window sizes. Clearly, it remains much to be done in this field.

In this study, our aim was to contribute to the knowledge on MSW properties: we wanted to find out whether it is possible to detect and analyse boundaries of different scales using the MSW analysis. First, we tested the capacities of the MSW on artificial data sets with known properties. Second, field data from a Hungarian mountain area were analysed in order to reveal boundaries and to extend our knowledge about vegetation pattern of the herb layer.

2. STUDY AREA

Our investigations were conducted on Mt Tubes (46°6′N, 18°12′E), which is the highest peak (611 m a.s.l.) in the Western part of the Mecsek Mts (southern Hungary) (Fig. 1A). Mean annual temperature is 8.8°C, mean annual precipitation is 723 mm (Szilárd 1981). Due to the northwest-southeast direction of the ridge of Mt Tubes, microclimate of the northern slope is cooler and moister than that of the southern slope (Horvát and Papp 1962, Lovász 1977). The bedrock consists of Triassic limestone, which is entirely covered by loess on the northern slope, but only partly covered on the southern one (Lovász and Wein 1974, Lovász 1977). The most characteristic soil type of the northern side is brown forest soil, whereas typical soil of the southern side is shallow rendzina (Lovász 1977).

The coolest parts of the northern slope of Mt Tubes are covered by mesic beech forests (Helleborus odorus-Fagetum), where Fagus sylvatica is by far the most abundant in the canopy layer. Shrub layer is almost entirely lacking. Dominant species of the herb layer is Allium ursinum, other typical species are Aconitum vulparia, Cardamine enneaphylla and Galeobdolon montanum (Horvát...
North-exposed slopes also harbour oak-hornbeam forests (Asperulo taurinae-Carpinetum). Here, Quercus petraea s. l. and Tilia tomentosa dominate the upper canopy, while Carpinus betulus forms the lower canopy layer. Among shrubs, Cornus mas and Crataegus laevigata are the most frequent. Abundant plants of the herb layer are Allium ursinum, Cardamine enneaphyllos, Carex pilosa, Corydalis cava and Melica uniflora (Horvát 1957, Morschhauser 1995). Where soil is shallow and stony, scree forests (Tilio tomentosae-Fraxinetum orni) have formed, the upper canopy of which consists mainly of Acer pseudoplatanus, Tilia platyphyllos and Tilia tomentosa, while in the lower canopy, Fraxinus ornus is typical. Characteristic species of the shrub layer is Cornus mas. Dominants of the herb layer are Allium ursinum and Mercurialis perennis (Morschhauser 1995). On the ridge of Mt Tubes, as well as on considerable parts of the northern slope, top-forests (Aconito anthorae-Fraxinetum orni) can be found. The canopy layer includes Fraxinus ornus and Quercus pubescens s. l. In the shrub layer, Cornus mas is especially abundant. Most typical plants of the herb layer are Allium ursinum, Corydalis solida, Helleborus odorus, Melica uniflora (Kevey and Borhidi 1998). The southern slope is occupied by a xeric mosaic complex consisting of shrubforests (Inulo spiraeifoliae-Quercetum pubescentis), rock swards (Serratulo radiatae-Brometum pannonici) and vergilius oak forests (Tamo-Quercetum virgilianae). The shrubforest (Inulo spiraeifoliae-Quercetum pubescentis) patches are formed by small groups of Fraxinus ornus and Quercus pubescens s. str. individuals. Among shrubs, Crataegus monogyna and Ligustrum vulgare are the most important, while Buglossoides purpureo-coerulea, Carex humilis, Geranium sanguineum and Inula spiraeifolia are typical in the herb layer (Morschhauser 1995). Rock swards (Serratulo radiatae-Brometum pannonici) are dominated by Bromus pannonicus; other frequent and abundant species are: Artemisia alba, Dictamnus albus, Inula spiraeifolia, Serratula radiata and Teucrium chamaedrys (Horvát 1946). The canopy layer of the vergilius oak forest (Tamo-Quercetum virgilianae) can be characterized by Fraxinus ornus and Quercus pubescens s. l. Shrub layer is primarily composed of Cornus

Fig. 2. A) Simulated species distribution patterns in the first artificial data set, representing ten community patches along a transect (80 species × 200 plots). Species are ordered into horizontal rows, plots into vertical columns. Within each row, presence of the given species is displayed in black, absence in white. B) Z-score (standardized Squared Euclidean Distance) profile of the first artificial data set. Peaks above the critical value in the graph indicate significant (P<0.05) boundaries.
László Erdős et al.

Mas, Lonicera caprifolium, Rosa arvensis, Ruscus aculeatus, Tamus communis and Viburnum lantana. Herb layer is very diverse, with species such as Brachypodium sylvaticum, Carex flacca, Helleborus odorus, Lathyrus niger, Viola alba (Morschhauser 1995).

Mt Tubes is a protected nature reserve. For the present study, the most typical and at the same time most intact part of Mt Tubes was chosen, where vegetation can be considered near-natural.

3. MATERIAL AND METHODS

3.1. Field studies

Our transect was established perpendicular to the ridge (Fig. 1B). Its position was chosen based on the vegetation map of the area (Morschhauser and Salamon-Albert 2001). The transect intersected the most typical plant communities of Mt Tubes. Transect length was 382 m, and it consisted of 1 m² contiguous plots. During field works, presence of all vascular plant species of the herb layer was recorded in July 2006 and in April 2007. Summer and spring records were combined for each plot before the analyses. As only the herb layer was sampled, our results apply only to this layer.

3.2. Artificial data sets

Two artificial data sets, simulating two possible vegetation patterns, were prepared in order to study the behaviour of the MSW method under different circumstances. Both data sets consisted of 200 plots and 80 species (Figs 2A, 3A).

In the first artificial data set, the transect was divided into two sections, both of them 100 m long, with different species composi-
Ecological boundaries at different scales

The two sections were separated by a boundary between plots 100 and 101 (with a considerable overlap). Both sections were divided into smaller patches. Note that the boundary between plots 100 and 101 is of a coarser scale than boundaries between the smaller patches. Species distributions near the boundaries were generated randomly so that probabilities of species occurrences decreased gradually away from the patch centres.

In the second artificial data set, the first section did not consist of smaller patches (Fig. 2B). Instead, species composition changed rather continuously along the transect until the boundary between plots 100 and 101. The second part of the transect was similar to that of the first data set. Again, there are boundaries of two different scales in the second artificial data set.

3.3. Moving split window analysis

Moving split window (MSW) technique (Webster 1978) was used to study the boundaries on both the artificial and the field data. As the first step of the MSW analysis, a ‘window’ is designated at one end of the transect. This window consists of two neighbouring plots. The window is then split into two halves, and the two halves are compared, based on a dissimilarity function. The window is shifted along the transect, and the dissimilarity function is computed in every position. When dissimilarity function is plotted against position, boundaries appear as peaks on the graph. Window size can be increased, thus analysis can be done at several spatial scales (Ludwig and Cornelius 1987, Körmöczi 2005). As dissimilarity function, we chose the Squared Euclidean Distance, which is the most commonly used distance metric in MSW studies (Johnston et al. 1992, Fortin and Dale 2005). Significance of the boundaries was tested after normalizing transformation (also called z-score transformation):

\[ Z = \frac{(d_{i,k} - d_{exp,k})}{SD_{exp,k}} \]  

where: \( z \) is the normalized score, \( i.e. \) z-score (standardized Squared Euclidean Distance), \( d_{i,k} \) is the Squared Euclidean Distance at position \( i \) if half-window size is \( k \), \( d_{exp,k} \) is the overall mean of Squared Euclidean Distance from randomized data for half-window size \( k \) (expected mean), and \( SD_{exp,k} \) is the standard deviation of the Squared Euclidean Distance values from the randomized data for half-window size \( k \) (overall mean and standard deviation were computed from 99 randomizations and for the whole transect). Randomization was made with random shift of species, during which distribution of each species was shifted a random number of units along the transect. Occurrences that were shifted beyond the end of the transect were wrapped back on to the opposite end (Palmer and van der Maarel 1995, Horváth 1998). In order to obtain a better understanding on the behaviour of the MSW as well as on the boundary characteristics, we applied three spatial scales by using different window-widths: for comparison, z-scores were averaged over 10–20, 30–40 and 50–60 window-widths, respectively. In the case of the field data, we also used a fourth scale, window-widths 70–80, which was enabled by the length of the transect. Window-widths 10–20 represent a fine-scale analysis: this scale roughly corresponds to the diameter of the small patches in both the artificial data sets (small patch diameter: 20 m) and in the field data (diameter of the patches on the southern slope: usually 5–25 m). Window–widths 30–40 tend to merge smaller patches, thus being an intermediate scale. Window-widths 50–60 and 70–80 represent a coarse-scale, which merge several neighbouring patches. Average z-scores were plotted against window mid-point position, resulting in a z-score profile. In the profile, vegetation boundaries appear as peaks. Peaks above 1.85 were regarded as indicating significant (\( P < 0.05 \)) boundaries (Körmöczi 2011). For the MSW-computations, we applied the statistical language R 2.10.1 (R Development Core Team 2009).

4. RESULTS

4.1. Artificial data

In the case of the first artificial data set, at window-widths 10–20 and 30–40, MSW was able to detect boundaries of both scales (Fig. 2B). However, the peaks of the z-score profile indicated only a small difference between the two boundary levels (that is, the boundaries between the small patches and
the boundary between the two 100 m sections of the gradient resulted in very similar peaks). It is clear that in real field situations, boundaries of different scales could not have been distinguished based on the z-score profile. In contrast, when window-widths 50–60 were used, the boundary of the coarser scale (between the two 100 m sections) was clearly distinguishable from the boundaries of the small patches. In this latter case, however, another problem arose: significance of the boundaries of the small patches dropped far below the significance level. Therefore, these boundaries would not have been identifiable if real field data had been used.

Situation was quite similar in the case of the second artificial data set (Fig. 3B). Again, using window-widths 10–20 or 30–40, MSW was able to detect all boundaries, but boundaries of different scales were hardly distinguishable. When window-widths 50–60 were applied, boundary between the two sections of the gradient was highly prominent, but boundaries of the small patches were not significant.

Thus we did not find window-widths which are capable of detecting all boundaries and at the same time differentiating between boundaries of different scales.

4.2. Field data

In the 382 plots, we found a total of 172 plant species. On the north-facing slope, larger patches of mesic communities were found, herb layers of which were generally rather

Fig. 4. A) Real species distribution pattern along the transect of Mt Tubes from field data. Species are ordered into horizontal rows, plots into vertical columns. Within each row, presence of the given species is displayed in black, absence in white. In the distribution pattern, only species occurring in at least five plots are displayed (122 species × 382 plots). B) Z-score (standardized Squared Euclidean Distance) profile of the transect from Mt Tubes. Peaks above the critical value in the graph indicate significant (P <0.05) boundaries.
similar. In contrast, we found small patches of xeric communities on the southern slope, with more different herb layers.

At window-widths 10–20 and 30–40, there were no significant boundaries on the northern slope (Fig 4B). In contrast, on the southern slope, relatively high and narrow peaks indicated sharp boundaries between habitat patches. At window-widths 50–60, a high and wide peak began to emerge between positions 267–274, while significance of all other peaks decreased (results not shown). At window-widths 70–80, only one prominent boundary remained, the one between plots 267–274.

The species distribution pattern showed that the transect could be divided into two sections with almost completely different species compositions (Fig. 4A). The major change between the two sections seemed to occur between plots 267–274: several species had their distribution limits here, and in this zone, species of both transect sections could be found.

5. DISCUSSION AND CONCLUSIONS

Our results emphasize that simulations can provide a useful tool to evaluate the potentials and limitations of the MSW, as was found by Brunt and Conley (1990) and Körmöczi (2005).

Our most important finding is that MSW is able to detect boundaries of different scales and it also can differentiate between coarse-scale and fine-scale boundaries. However, this is only possible if several window-widths are used: at small window-widths, all boundaries are detected, but boundaries of different scales can not be separated. At greater window-widths, boundaries of coarser scales appear as conspicuous peaks, but boundaries of finer scales tend to disappear (Figs 2B, 3B).

Based on the MSW analyses of our field data deriving from the Mecsek Mts, we found that herb layer vegetation pattern of Mt Tubes resembles our second model given in Fig. 3. There is a series of continuously intergrading mesic communities on the northern side of the gradient, with gradually changing species compositions. On the southern end of the gradient, there are relatively sharp boundaries between different xeric communities of a mosaic pattern. This can probably be explained by the effects of the canopy cover on the herb layer: on the southern slope, patches with high canopy cover values alternate with patches without a canopy layer. This has major influences on the microclimate, which in turn affects the species composition of the herb layer. Similar controlling mechanisms may operate in the nearby Villány Mts (cf. Erdős et al. 2012).

MSW clearly indicates that there are boundaries of two different scales in the vegetation of Mt Tubes. First, there are boundaries between community patches of the southern slope. Second, another boundary of a coarser scale can be found between plots 267–274 (Fig. 4B). This latter boundary is a transition zone between two community complexes (the mesic series and the xeric mosaic).

The vegetation pattern and the boundaries identified by our examination can be fit into the system established by van der Maarel (1976). The series of mesic communities on the northern side of the gradient may be treated as a continuum, whereas there are sharp ecotones between the patches of the xeric mosaic on the southern end of the gradient. The boundaries of the finer scale are boundaries between phytocoenoses and the one of the coarser scale is a boundary between phytocoenose complexes, as mentioned by van der Maarel (1976).

Vegetation gradients have already been studied in the Mecsek Mts (Morschhäuser 1995, Kevey and Borhidi 1998). However, these studies used classical coenological methods, and were carried out at one single spatial scale. Thus, information about boundary patterns and transitional phenomena was very limited.

In a former study, Kevey and Borhidi (1998) found that the main transition zone between the mesic and the xeric communities on Mt Tubes is the top-forest (Aconito anthorae-Fraxinetum orni). In contrast, we found that the boundary is located on the southern slope, in the vergilius oak forest (Tamo-Quercetum virgilianae) (between plots 267–274, Fig. 4). The explanation of this is that the top-forest (Aconito anthorae-Fraxinetum orni) has xeric canopy and shrub layers but a mostly mesic herb layer (Kevey and Borhidi 1998). Therefore, if only the herb
layer is studied, as was the case in the present study, the top-forest (Aconito anthorae-Fraxinetum orni) is similar to the mesic communities of the northern slope. The major change in species composition occurs a bit farther to the south, in the vergilius oak forest (Tamo-Quercetum virgilibanae).

In a herb layer vegetation analysis using ecological indicator values, Morschhauser and Salamon-Albert (2001) found that transition between mesic and xeric sites occurs on the southern slope of Mt Tubes, between the top-forest (Aconito anthorae-Fraxinetum orni) and the vergilius oak forest (Tamo-Quercetum virgilibanae). Moreover, soil reaction values seem to change even farther down on the southern slope. These results are in fairly good agreement with the major peak of the MSW-profile of our analysis (Fig. 4), which is also located on the southern slope.

In this study, MSW provided an insight into vegetation patterns of the Mecsek Mts and efficiently supported former vegetation studies. We suggest that it could be used in similar mountain areas in order to analyse gradients and detect boundaries at multiple scales, improving our understanding of vegetation patterns. However, application of greater plot sizes may be necessary in mesic forests, which could possibly support more efficient boundary detection.

6. REFERENCES


Received after revision February 2013