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On the terms related to spatial ecological gradients and boundaries

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ABSTRACT   Ecological gradients and boundaries are currently in the focus of research interest. A widely accepted terminology, however, is still lacking, thus the use of the terms related to gradients and boundaries continues to be confusing. In this paper, we provide new more elaborated definition of the spatial boundary. We distinguish between the gradient (transition) and the space-segment (transitional zone). Our paper identifies the main difference between the two types of gradients: cline and tone. We discuss the meanings of the synonyms boundary line, boundary zone, edge, margin and border. We review the importance of scale and organizational levels in the field of gradients and boundaries. The article also enlightens the difficulties of vegetation mapping associated with boundaries. At last, we identify some important research topics for the future, where intensive studies are needed   **Acta Biol Szeged 55(2):279-287 (2011)**

Ecological boundaries and gradients belong to the most current research topics in ecology. Although the area occupied by the boundaries may be small compared to the total landscape or habitat (Cadenasso et al. 2003a), their role is extremely important, because they control the flow of organisms, materials, energy, and information (Wiens et al. 1985; Wiens 1992; Cadenasso and Pickett 2001; Cadenasso et al. 2003b; Strayer et al. 2003). Boundaries can have significant effects on the adjacent patches they separate. According to Fagan et al. (1999), boundaries can influence the within-patch interactions between populations, for example competition or consumer-resource dynamics.

Knowledge about ecological gradients and boundaries plays a significant role in the fields of community ecology and landscape ecology, as well as in nature conservation (Yarrow and Marín 2007). Increased fragmentation due to human activity results in more boundaries (Merriam and Wegner 1992; Boren et al. 1997; Standovár and Primack 2001; Pullin 2002). Responses of boundaries to global changes, especially to global climate change will probably be one of the most important research questions in the upcoming decades (Holland 1988; Weinstein 1992; Neilson 1993; Allen and Breshears 1998; Weltzin and McPherson 2000).

Increasingly confusing is the inconsistent use of the terms linked with boundaries and gradients. A widely accepted terminology is lacking (Jagomägi et al. 1988; van der Maarel 1990; Kolasa and Zalewski 1995; Kent et al. 1997; Baker et

al. 2002; Kark and van Rensburg 2006), so it is often difficult to compare the studies carried out by different researchers (Hufkens et al. 2009).

In this paper, we summarize the opinions of several authors, and make an attempt to define the following terms: boundary, boundary line, boundary zone, ecotone, ecocline, edge, margin and border. We also discuss some respects of scales and organizational levels. The article illustrates the difficulties of depicting boundaries on vegetation maps and briefly discusses some possible solutions. Furthermore, we identify some possible research directions where active investigations are most urgent.

Mismatch between nature and our words

A basic property of our thinking is the categorization of things (Proctor 1974; Standovár 1995; Podani 1997). Grouping into categories involves a simplification of the immeasurable variety of nature. This simplification is a consequence of the mismatch between reality and our words (Sainsbury 1995): our words denote discrete categories, while reality does not necessarily come in discrete entities. However, we have to use words that denote discrete categories, because this is the cost we have to pay for finding our way around the world.

Delineation of a boundary between two communities (for example when we draw conventional vegetation maps) is a categorization with spatial constraint. Delineating the boundary involves a simplification of reality. Boundaries are regarded as having no thickness (Zonneveld 1974). The contrast between the two patches (the dissimilarity between the two units) is increased by the map and the patches are

considered homogenous (Küchler 1974). Thus, classification maps produce oversimplification, because neither gradual changes in the proximity of the boundary nor within-patch inhomogeneities are taken into account.

To reduce such oversimplification, a transitional zone can be drawn on the map between the two neighbouring units (e.g. an edge between a forest and a grassland). In this case, the problem of where to delineate the boundaries of this zone emerges (Csorba 2008).

The cause of the difficulty is that our words referring to vegetation units denote discrete categories, whereas vegetation does not form discrete entities or at least is discrete and continuous at the same time.

Boundary, boundary line, boundary zone

There are three meanings of the term boundary: a temporal, a spatial (topographical), and an abstract (topological) one.

Temporal boundaries can denote rapid changes in time (Westhoff 1974). During succession, communities of a given locality change, and the question can arise, from what point of time changes are sufficient to speak about another community (Gleason 1926; Jax et al. 1998).

Abstract boundaries exist not in a topographical, but in a topological space. Objects are grouped not necessarily with reference to their spatial relationships (that is, two objects that are near to each other in the abstract space may be far in the real space). In vegetation science, such abstract categories are associations. When delineating the abstract boundary of an association, we must determine which association a plot or stand belongs to (Gleason 1926; Proctor 1974; Westhoff 1974; Zonneveld 1974; Ramenskii in Rabotnov 1978).

Boundaries are most frequently defined in the spatial sense. Henceforth we will consider spatial boundaries exclusively. A spatial boundary always separates two neighbouring space-segments (van der Maarel 1976; Cadenasso et al. 2003b; Martín et al. 2006; Peters et al. 2006). The two neighbouring space-segments have to be different from each other from the point of view of the research question (Canny 1981; Cadenasso et al. 2003b; Fagan et al. 2003; Martín et al. 2006; Peters et al. 2006). Difference is offset within the boundary zone (that is, transition occurs here), therefore, gradients within the boundary are always steeper than in either of the neighbouring space-segments (Cadenasso et al. 2003b). The boundary not only separates but also connects, because a boundary through which no fluxes occur probably does not exist in nature (Wiens et al. 1985). The thickness of a boundary is necessarily smaller than the width of the neighbouring patches (Kolasa and Zalewski 1995; Körmöczi and Jusztin 2003; Csereklye et al. 2008).

The definition of the spatial boundary can be given as follows: 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.

In accordance with the previous definition, if the two sides of the boundary do not differ, there is no boundary at all. In contrast to Hansen et al. (1988) and Cadenasso et al. (2003a), a hedgerow, a windbreak, a fence or a road is not necessarily a boundary. If these objects are situated in a homogenous matrix (that is, the patches separated by these objects do not differ), or if no transition occurs within them, they are simply landscape elements (van der Maarel 1990) or corridors (Forman 1995). Although corridors and boundaries are to some extent similar in their functions, they differ fundamentally in their structure (Forman 1995).

Boundaries between communities can be relatively sharp or blurred (Gleason 1926; Paczoski in Dąbrowska-Prot et al. 1973; Kent et al. 1997). Boundaries that are sharp at every spatial resolution do not exist. When the resolution gets finer, every boundary becomes blurred (Strayer et al. 2003). A boundary that is like a line at a given resolution will be a zone at a finer resolution (Cadenasso et al 2003b). Of course, at this finer resolution, boundary zones themselves have two boundaries (Kolasa and Zalewski 1995). According to Armand (1992): "Any natural boundary is in reality a transition zone, which has its own two boundaries. They are, in turn, also transition zones with their own boundaries, and so on, endlessly." In short, delineating lines does not correspond to reality, because transitions are gradual (Csorba 2008).

The very same boundary can appear as a line or as a zone, depending on the resolution. The phrases boundary line (Grenzlinie) and boundary zone (Grenzzone, Grenzbereich) (van der Maarel 1976; Forman and Moore 1992) refer to this strange duality.

If the resolution is coarse enough, a community boundary may appear on a map as a line (a one-dimensional object). But every boundary continues below and above the surface, and – as mentioned above – every boundary has width. Therefore, boundaries are three-dimensional structures, with lenght, height, and thickness (van der Maarel 1976; Kolasa and Zalewski 1995; Cadenasso et al. 2003a).

Community gradients and environmental gradients

If we study ecological gradients, it is necessary to distinguish between community gradients (where a kind of change in species composition occurs in space) and environmental gradients (where a kind of change in environmental factors occurs in space). (Of course, population gradients also belong to ecological gradients, but in this paper, we consider only community gradients.) However, it is confusing, that the words ecotone and ecocline are used for both community gradients and environmental gradients. It is clear, that we

Table 1. Terms in the literature denoting environmental gradients and community gradients.

	environmental gradient	community gradient
Küchler (1974), Juhász-Nagy (1986)	ecocline	coenocline
Zólyomi (1987)	ecotone	coenotone
Whittaker (1967, 1975)	complex-gradient, factor-gradient	coenocline
Jagomägi et al. (1988)	causal ecotone	resultative ecotone
Fortin et al. (2000)	environmental ecotone	biotic ecotone

need a term to denote community gradients, and another term to denote environmental gradients. For this purpose, several expressions have been coined (Table 1).

The twin-terms coenocline and ecocline (Küchler 1974; Juhász-Nagy 1986), as well as coenotone and ecotone (Zólyomi 1987) were suggested in Central Europe. Coenotone and coenocline denote the community gradients, while ecotone and ecocline refer to the gradients of the background factors that cause the community gradients.

The terms coenocline and ecocline were already used by Whittaker (1967, 1975), but he used the following terminology: an ecocline is a gradient of ecosystems, that is, a community gradient together with the environmental gradients. In Whittaker's view, a complex-gradient is a gradient of environmental complexes, *i.e.* a gradient of several environmental factors, whereas a factor-gradient is a gradient of a simple environmental factor. Whittaker's fourth term, coenocline denotes a community gradient.

Albeit the words coenotone and coenocline seem to be appropriate to denote community gradients, they were used mainly in the 1970's (Gauch and Whittaker 1972; Westhoff 1974, Noy-Meir 1978; Phillips 1978), whereas nowadays these terms are rarely used (Kleinebecker et al. 2007). It is important to note that the words coenotone and coenocline are often used to denote abstract (that is, topological), and

not topographical gradients (for an obvious example, see Zólyomi 1987).

Instead of the above mentioned terms, we may use the phrases of Jagomägi et al. (1988): causal ecotone and resultative ecotone (the first term meaning an environmental gradient and the second a community gradient).

Another possiblity is to use the terms of Fortin et al. (2000): biotic and environmental ecotones. Biotic ecotones or ecoclines refer to the community gradients, whilst environmental ecotones and ecoclines mean the gradients of the background factors.

Gradient and zone

A prerequisite of the elimination of the terminological confusion is the distinction between the space-segment and the transition within this space-segment (Erdős et al. 2010). The transition (the gradient) cannot be identical with the transitional zone (a space-segment) (Fig. 1). It is confusing in the literature that the terms ecotone, ecocline, coenotone, and coenocline can denote transitions (*i.e.*, gradients), or transitional zones (*i.e.*, boundaries, space-segments), or both.

Ecotone and coenotone most often denote zones (Clements 1907; van der Maarel 1976; Mészáros et al. 1981; Holland 1988; Jagomägi et al. 1988; Mirzadinov 1988; Swanson et al. 1992; Gosz 1993; Baker et al. 2002; Lévêque 2003), but occasionally zones and gradients at the same time (Odum 1971). The opposite can be seen in the case of the terms ecocline and coenocline, which usually denote gradients (Whittaker 1967, 1975; Phillips 1978; Ricklefs 1980; Kleinebecker et al. 2007) and not very often space-segments (van Leeuwen 1966; van der Maarel 1976) or both (Jeník 1992; Kent et al. 1997).

This difficulty can be solved by using the original meanings of the words tone and cline. The terms ecotone, ecocline, coenotone, and coenocline should be used to denote gradients, and not space-segments! The Greek root "tonus" in the words ecotone and coenotone means tension (Harris 1988; Mirzadinov 1988; Kark and van Rensburg 2006), that is, a gradient between two neighbouring units. The word cline, introduced by Huxley (1938), originally means a gradual transition, a gradient. Westhoff (in van der Maarel 1976) writes: "A vegetational cline is a gradual transition in space of one vegetation type to another."
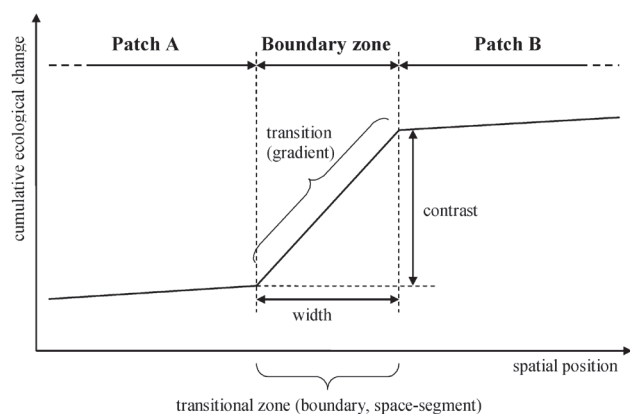

Figure 1. Terminological distinction between transition and transitional zone, and constituents of sharpness (abruptness): contrast and width.

Different terms should be used for the space-segment and the transitions within this space-segment (Fig. 1). While the boundary is a space-segment, ecotone and ecocline (as well as coenotone and coenocline) are gradients within a space-segment. The gradient is steep in the case of the tone, and it is gradual in the case of the cline. However, as we will see in the next chapter, there are gradients of intermediate steepness and no sharp line exists between tone and cline.

Since these terms denote gradients, they should not be regarded as types of boundaries. For example, if we want to speak about a relatively sharp boundary we should not use the word ecotone. Instead, application of one of the following phrases is suggested: ecotone zone (Churkina and Svirezhev 1995), ecotonal boundary or simply sharp boundary. Similarly (if the gradient within the boundary is more gradual), ecocline zone, ecoclinal boundary or blurred boundary should be used.

Ecological (both community and environmental) gradients can occur within or outside boundaries. A cline, for example, can refer to a whole series of communities along a gradient (Fig. 2a.), but also to a gradual and blurred transition between two contacting communities (Fig. 2b.) (Whittaker 1975). Of course, in both senses there is a gradient, but at different scales. Figure 2a. shows a cline from community A to community E. This gradient of communities is independent of a boundary situation. In Figure 2b., the cline can be found in the space-segment denoted with B. Here, the community gradient is a transition from community A to community C. In this case, the community gradient occurs within the boundary. (Whether B can be recognized as a separate community, is disputable, see below.)

Differences between limes convergens and limes divergens

According to van Leeuwen (1966) and van der Maarel (1976, 1990), two main types of boundaries exist: limes convergens (ecotonal boundary) and limes divergens (ecoclinal boundary). Limes convergens is a boundary where several species reach their distributional limits within a narrow zone, forming an abrupt boundary. In contrast, where distributional limits of the species are not so close, a limes divergens develops. Limes convergens and limes divergens can be distinguished based on three attributes: sharpness (abruptness) of the transition, stability of the environmental factors within the boundary, and species diversity: limes divergens is less sharp, more stable and more diverse (van der Maarel 1976, 1990; van Leeuwen 1966).

In the followings, we shall discuss the applicability of the above attributes in distinguishing between limes convergens and limes divergens. According to van Leeuwen (1966) and van der Maarel (1976, 1990), diversity is high only in ecoclinal boundaries, while the diversity of ecotonal boundaries is low. However, there are few studies which support this
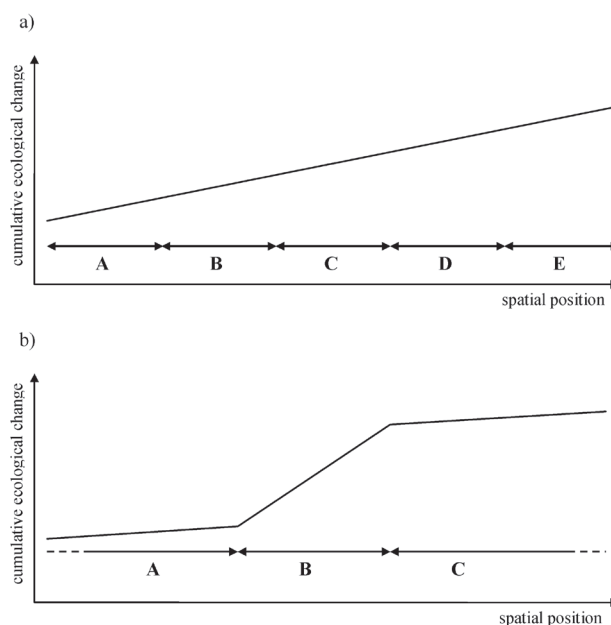

Figure 2. Cline, as community gradient. A cline may be a continuous change of a series of communities (a) or a gradient between two communities (b). In the first case A-E are the communities, and in the second case A and C: communities, B: space-segment of the cline.

view. In fact, results are often contradictory (Kark and van Rensburg 2006; Erdős et al. 2011). Moreover, evaluation of the studies is complicated, because authors often do not differentiate between ecotonal and ecoclinal boundaries, so we can not know which boundary type the measured diversity was observed in. Therefore, species diversity within boundaries can not be used in differentiating between limes convergens and limes divergens.

Two attributes remain: stability and sharpness. However, by drawing the types and sub-types of the boundary zones established by van Leeuwen (1966) in a coordinate system, it is obvious that the main difference is in sharpness (Fig. 3). Indeed, most researchers consider ecotonal boundaries to be sharp and ecoclinal boundaries to be blurred (Zonneveld 1974; di Castri and Hansen 1992; Jeník 1992; Kent et al. 1997; Hennenberg 2005).

Sharpness has two constituents: contrast and width (Fig. 1). Contrast means the difference of the communities or environmental factors between the neighbouring patches (Cadenasso et al 2003b; Strayer et al. 2003). The width of the zone is the size of the space-segment in which the difference is offset. The greater the contrast of the neighbouring patches and the smaller the width of the boundary, the greater the sharpness.

Both van Leeuwen (1966) and van der Maarel (1976) emphasize that ecotonal boundary and ecoclinal boundary are extreme types of boundaries between which intermedi-
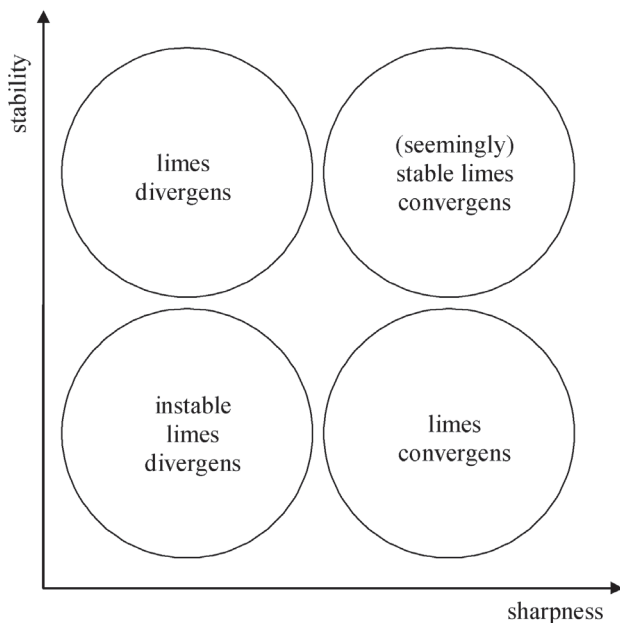
Figure 3. Types of boundaries according to van Leeuwen (1966) in a coordinate system.

ate kinds are possible. Real boundaries identified in nature can be placed on a continuum, the endpoints of which are limes convergens (ecotonal boundary) and limes divergens (ecoclinal boundary).

In sum, tones and clines are gradients; a tone means a steep gradient, while a cline is gradual. There are environmental gradients (*i.e.*, the gradients of the background factors) and community gradients. If we want to speak about boundaries, we should use the phrases ecotone zone, ecotonal boundary or simply sharp boundary (and ecocline zone, ecoclinal boundary or blurred boundary).

Edge, margin, border

The terms edge and boundary are often used as synonyms (Brunt and Conley 1990; Gosz 1991; Laurance et al. 2001; Cadenasso et al. 2003b; Csereklye et al. 2008; Erdős et al. 2011). Margin is also used in the same meaning (e.g. Risser 1995; Kivistö and Kuusinen 2000). It is important to note that edge and edge effect are not the same, as discussed more detailedly in Erdős et al. (2010).

The term border is relatively rarely used in the literature. It usually suggests a thin boundary (Jagomägi et al. 1988; Łuczaj and Sadowska 1997). In our opinion, the word border should be regarded as synonymous with the terms boundary and edge. Moreover, the terms borderline (e.g. Dutoit et al. 2007) or border area (e.g. van Leeuwen 1966) can be used depending on whether the border appears as a line or as a zone at the given resolution.

The importance of scale and organizational levels

The importance of hierarchy and the related topics of scale and organizational levels is widely recognized in ecology (cf. Allen and Starr 1982). Consequently, spatial scales and organizational levels must not be neglected in the case of ecological gradients and boundaries.

Ecological gradients and boundaries occur at severel spatial scales and organizational levels (Holland 1988; Hansen et al. 1988; Jagomägi et al. 1988; Gosz and Sharpe 1989; Gosz 1991, 1993; diCastri and Hansen 1992; Johnston et al. 1992; Risser 1995; Strayer et al. 2003; Peters et al. 2006). For example, according to Peters et al. (2006), ecological boundaries exist between individual plants, between patches of plant populations, and between plant associations. Rusek (1992) distinguishes microecotone, mesoecotone and macroecotone. At the edge of a moss cushion a microecotone can be found, a forest edge is a mesoecotone, whereas biom boundaries form macroecotones. (Ecotone is used in this cited article, as well as in several other articles, as synonymous with boundary.) Szwed and Ratyńska (1991) regard boundaries between plant associations as microecotones and boundaries between vegetation formations (~biomes) as macroecotones. Gosz (1993) identifies five ecotone levels ranging from the individual plants to the biomes.

Gosz and Sharpe (1989) and Gosz (1991, 1993) suggested that different constraints may be responsible for the control of boundaries at different scales. Broad-scale boundaries (e.g. biom boundaries) are formed by climatic parameters (temperature and moisture), whereas the characteristics of fine-scale ecotones are probably determined by site-specific parameters such as soil discontinuities (Gosz and Sharpe 1989; Gosz 1991). Moreover, the number of constraints is increasing towards finer scales, which contributes to the difficulties in the study of fine-scale boundaries (Gosz 1993).

Both the boundary width's order of magnitude and the organizational rank of a given boundary must be lower than those of the two neighbouring units (Mirzadinov 1988). As we have noted earlier in the present article, a boundary must be considerably narrower than the neighbouring patches (Kolasa and Zalewski 1995; Körmöczi and Jusztin 2003; Csereklye et al. 2008). To put it another way, its order of magnitude has to be lower. If boundaries were allowed to possess a width of the same order of magnitude as the neighbouring units, huge amounts of the Earth's surface could be categorized as boundaries (cf. Csorba 2008). This not only would contradict the intuitive meaning of the term boundary, but it would also be undesirable since situation would be hard to manage. The organizational rank of a boundary should also be lower than that of the two contacting units. For example, the boundary between two formation types (e.g. forest and grassland) may be at the association level, whereas the boundary between two associations is at a lower level (Szwed and Ratyńska 1991).

As noted by Jeník (1992), ecotonal structures are only rarely treated as separate plant associations due to their spatial restriction, although considerable debates exist in this respect, mainly in the case of forest edges (cf. Papp 2007).

It depends on the scale whether an entity is recognized as a boundary or not (Küchler 1974; Kolasa and Zalewski 1995). In fact, what is a boundary at a given resolution may be studied as consisting of patches with their own boundaries at a finer resolution (Hansen et al. 1988; Peters et al. 2006). Thus a boundary often has a mosaic structure. Patches dominated by one plant species are quite large in the interior area of a biom, because that plant species can occupy several microhabitats. Approaching the boundary of the biom, more and more species reach their limits of ecological tolerance. Therefore, suitable microhabitats begin to diminish and, as a consequence, patches decrease in diameter. As a result, boundaries often show increased numbers of small patches of plant species (Gosz 1991, 1993). The same phenomenon was observed at much finer scales (Bagi 1997).

Boundaries and vegetation mapping

It is a commonplace that in nature, one can find mosaics consisting of patches. Patches are delimited by boundaries (Laurance et al. 2001; Cadenasso et al. 2003b). Vegetation mapping involves delineating those boundaries (Küchler 1974; Bagi 1997, 1998).

The Zürich-Montpellier phytosociology school (the most wide-spread phytosociology school in Central Europe) implies that vegetation units are discontinuous, that is, their boundaries are relatively sharp (Bagi 1998; Fekete 1998). In fact, as noted earlier, if the resolution of the map is coarse enough, a simple line is appropriate to denote a boundary (Bagi 1997; Csorba 2008). However, if the boundary is blurred and wide at the given resolution, considerable problems arise in vegetation mapping (Lájer 2000). The wider a transition zone, the more complicated to delineate a boundary (Küchler 1974).

If boundary zones are treated as units of their own, vegetation mappers face serious problems. First of all, boundaries with a transitional species composition have no coenological standards, that is, they can not be classified into existing syntaxonomical categories (Bagi 1991, 1997; Seregélyes and Csomós 1995). Second, boundary delineation is vague due to the bistability of perception (Bagi 1997, 1998). Boundaries of species-rich communities are likely to result in greater vagueness (Bagi 1998). Third, floristic composition of boundary zones is highly variable, depending on which of the neighbouring units has a greater influence on it (Bagi 1998).

One possible solution is to give the boundary zone a name as a combination from the names of the two adjoining units (Bagi 1998), which also emphasizes the transitory character of the boundary zone. A second option is to divide the boundary zone into narrow stripes (Bagi 1997). A drawback of this latter method is the very big number of newly created categories (Bagi 1998). According to Küchler (1974), in some instances it is reasonable to omit boundaries on vegetation maps. An excellent example was given by Schmidtlein et al. (2007). In their vegetation map of a mosaic habitat complex in Germany, each pixel had the chance to represent a particular species composition with a unique colour. Thus the method reconciles vegetation mapping and complex reality. However, although this new approach may be promising, conventional vegetation maps depicting boundary lines will be indispensable in several cases (Schmidtlein et al. 2007).

The concept of gradients

There are many concepts related to ecological gradients and boundaries, such as ecotone, ecocline, edge etc. Yarrow and Marín (2007) suggested that the concept of transitional zone is the most general. In our opinion, the concept of gradients deserves consideration, since it is even more general than the concept of transition zones. According to this point of view, not only boundary areas but also other regions can be conceived as consisting of horizontal gradients. There are within-patch and between-patch gradients everywhere. In this sense, the main difference between boundaries and other areas is that the gradient in the boundary is much steeper than elsewhere (Goodall 1963; Whittaker 1967; Cadenasso et al. 2003b). Moreover, the difference between sharp and blurred boundaries lies in the steepness of the gradient in the boundary. This thinking is not confined to one dimension: a gradient in one direction becomes a pattern in more than one direction (Whittaker 1967), that is, every pattern consists of gradients.

Future directions

We identified a number of gaps in the ecology of gradients and boundaries both in theory and practice.

First of all, more long-term studies would be needed in order to gather information on the dynamics of vegetation, including the dynamics of boundaries (cf. Bartha 2008), which is especially important if we want to predict the responses of boundaries to global changes, especially to global climate change.

One of the most important research topics for the future is to link boundary structure with boundary function (Cadenasso et al. 2003a). By this time, it is poorly understood, how structural characteristics of the boundaries determine functions (e.g. diversity, permeability).

There are models predicting responses of variables (e.g. abundance of a species) to edges. For example, Ries et al. (2004) suggested that edge responses depend on the resource distribution between adjoining communities. Although their model proved to perform well, it is clear that much more case studies would be necessary.

Edges may play an important role in nature conservation,

e.g. in the survival of protected and rare plants (cf. Erdős et al. 2011). However, our knowledge is far from being sufficient. For example, the role of transitional areas in the preservation of relict species is judged contradictorily (cf. Zólyomi 1987; van der Maarel 1990).

The definition of edge species is lacking (Lloyd et al. 2000), and there are too few data on the exinstence of edge-related species (cf. Erdős et al. 2011).

Although there are some theories concerning the similarity of temporal and spatial gradients (Whittaker 1967, 1975; Margalef 1979; Neilson 1993; Huntley and Baxter 2006), the connections between the dimensions of space and the dimension of time on the field of ecological gradients have not been studied intensively so far.

Vertical gradients (i.e. gradients between vegetation layers) form another neglected research area, since most studies focus on horizontal gradients.

It was realized early (Ramenskii in Rabotnov 1978) that sometimes abrupt changes in vegetation occur in spite of continuous changes in the environment. Further studies are needed to reveal the possible explanations for these phenomena (for some possible reasons, see Weltzin and McPherson 1999; Fagan et al. 2003; Holt et al. 2005).

One of the most controversial issues in ecology is diversity within boundary habitats. The most wide-spread hypothesis states that diversity is greater in boundary zones than in either of the two contacting communities (e.g. Odum 1971; Pianka 1983; Chiras 1991). Other theories claim that only blurred boundaries support higher diversities, while sharp ones are less diverse compared to the two adjoining communities (e.g. van Leeuwen 1966; van der Maarel 1976, 1990; Brown and Gibson 1983). Unfortunately, field studies concerning plant species diversity within boundary zones are relatively scarce.

Generalizations in the issues mentioned above will be possible only if the different studies are comparable. In our opinion, it would be necessary to describe the key boundary features (the most imortant of them being contrast and width) as precisely as possible in every case study and to use a terminology free from inconsistencies. We hope that the present article has contributed to the elaboration of this new terminology.

Acknowledgements

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