ECOTONES: MARGINAL OR CENTRAL AREAS OF TRANSITION?

Salit Kark[a,*] and Berndt J. van Rensburg[b]

[a]*The Biodiversity Research Group, Department of Evolution, Systematics and Ecology, Alexander Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Jerusalem 91904, Israel*
[b]*Department of Zoology and Entomology, Centre for Invasion Biology, University of Pretoria, Pretoria 0002, South Africa*

ABSTRACT

Areas of environmental transition, where ecological communities coincide, are sometimes termed ecotones. These regions often correspond with sharp environmental gradients. Ecotones occur at multiple spatial scales, ranging from transitions between biomes to local small-scale transitions. In recent years ecotones have received increasing scientific attention after being neglected for years, as studies historically often focused on distinct communities. However, it is still debatable whether these transitional regions are speciation and biodiversity hotspots that deserve special conservation interest or are actually areas that hold marginal populations that depend on other parts of the range for the maintenance of their biodiversity and therefore should not deserve primary investment. This paper discusses some of the recent advancements in our understanding of the role of ecotones in ecology, evolution, and conservation.

Keywords: boundaries, boundary detection methods, ecotones, review, transitional environments

INTRODUCTION

Understanding the mechanisms, both biological and anthropogenic, that account for changes in environmental variables and that translate into altered species richness and species turnover (β-diversity) patterns in space and time has been a cornerstone in ecological, evolutionary, and conservation research for many years (Pimm et al., 1995). Over the years, investigations tended to focus on distinct ecosystems and communities (e.g., Mediterranean, grasslands, boreal) (Holland et al., 1991; Risser, 1995a; Smith et al., 2001). However, areas of transitions between ecological communities (also termed ecotones) have received much less attention in biodiversity research. Recent studies that incorporated the dynamic nature of the environment (i.e., adopted a non-static approach) when examining the way in which global change may affect biodiversity patterns, and the conservation implications thereof, have increased the interest in these areas. Are

ecotones dynamic biodiversity hotspots where novel and unique evolutionary forms are generated and are maintained? Are they centers of speciation? Do richness and/or rarity peak in ecotones? Are there ecotonal species? Are ecological transition zones spatially congruent among taxa? Should these areas receive high, or rather secondary conservation priority?

Areas of transition between more homogenous communities often correspond with sharp environmental and ecological gradients. These areas are often depicted by the responses of plant communities. Consequently, because of the great influence of dominant plants on ecosystem structure (Gosz, 1993; Risser, 1995a), ecosystem properties and animal communities are believed to respond in parallel, and there is accumulating evidence suggesting that at least in some cases, plant- and animal-based ecotones are congruent (e.g., Boone and Krohn, 2000; Gaston et al., 2001; van Rensburg et al., 2004). Ecotones occur at multiple spatial scales, from global-scale transitions between major biomes to small-scale ecotones where local vegetation communities and microhabitats coincide (Gosz, 1993; Risser, 1995a) (Fig. 1). Ecotones also show a diversity of boundary types that range from natural boundaries (e.g., altitudinal, latitudinal transitions) to human-generated ecotones (e.g., forest clear-cut edges or urban ecotones). The location and characteristics of transitional areas can be shaped by both biotic and abiotic factors (Fortin et al., 2000). Fortin et al. (2000) distinguished between environmental and biotic ecotones. Environmental ecotones correspond to sharp physical changes in environmental factors (e.g., soil, rainfall). Biotic ecotones reflect species responses to environmental change and/or to species interactions, and can be identified at the species, community, or ecosystem levels.

a   b   c
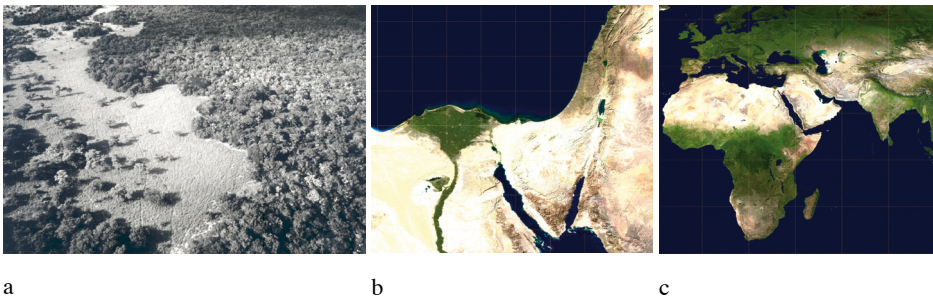
Fig. 1. (a) Local ecotones—Sharp ecotone between sand forest and mixed woodland along the southern Mozambique Coastal Plain of Northern KwaZulu-Natal in South Africa. Photo by Berndt J. van Rensburg (b) Regional ecotones—Satellite image showing Mediterranean-desert and ecotones in the Middle East. Source: NASA Goddard Space Flight Center. Image by Reto Stöckli (land surface, shallow water, clouds). Enhancements by Robert Simmon (ocean color, compositing, 3D globes, animation). Downloaded from http://earthobservatory.nasa.gov/Newsroom/BlueMarble/ (c) Global ecotones—Ecotones in the Sahel Region. Source: NASA Goddard Space Flight Center (see regional ecotones).

A BRIEF HISTORY OF ECOTONES

The origin of the word "ecotone" is in the Greek roots "oikos" (home) and "tonus" (tension). Its original reference was to a tension zone where plant communities adjoin (Curtis, 1959; Gosz and Sharpe, 1989; Kent et al., 1997). A conceptual ecological framework for the study of ecotones was given over fifty years ago by Odum (1953): "An ecotone is a transition between two or more communities; it is a junction zone or tension belt which may have considerable linear extent but is narrower than the adjoining community areas themselves."

Beginning with Clements (1897, 1905) and Livingston (1903) and continuing with Leopold (1933), there has been interest in boundary regions and edges of ecological systems. Odum (1953) suggested increased richness and abundance in ecotones and the occurrence of unique ecotonal species, what has also been called the "ecotone effect". Up to the 1970s there was considerable interest in ecotones in the scientific community (Lidicker, 1999). Until the mid-1980s, this interest subsided and a focus on more homogenous and well-defined ecosystems and communities (e.g., Mediterranean regions and boreal forests) became common (as reviewed by Lidicker, 1999). For example, five of eight general ecology textbooks from this period did not even mention the term ecotone, and only one of the eight discussed ecotones in more than a paragraph. A revival of the field began in the late 1980s and 1990s, when its relevance to new research areas, and especially conservation biology and global change biology, became recognized (di Castri et al., 1988). Studies on ecotones in the 1980s often focused on material flow (e.g., water, nutrients) across communities and on ecosystem processes (Risser, 1995b), as emphasized in a series of SCOPE (Scientific Committee on Problems of the Environment) meetings in the late 1980s (di Castri et al., 1988; Risser, 1993).

Today it is widely accepted that a clear understanding of ecotones and the areas they border, as well as identification of the regional biotas to which assemblages belong, are important for understanding the processes that are responsible for shaping the distribution and abundance of organisms (Gosz, 1992; Risser, 1995a; Williams, 1996; Srivastava, 1999; Williams et al., 1999). At large scales, ecotones have been used to define the spatial boundaries of biogeographical regions, which in turn have formed and continue to form a significant, though often contentious, basis for understanding the evolutionary history of life on Earth (see Cox, 2001; Morrone, 2002). For example, the relationship of the biotas and areas surrounding the Wallace Line has been one of considerable importance, though surrounded by controversy (Darlington, 1957; Cox, 2001). At smaller scales, sharp discontinuities and the relatively homogenous regions between them are often used to demonstrate regional faunal complexity that may require either historical or ecological explanation (see, e.g., Poynton, 1961; Poynton and Boycott, 1996; van Rensburg et al., 2000), and to better understand finer scale assemblage or community structure and the properties of community members (Bestelmeyer and Wiens, 2001). From a more pragmatic perspective, delineation of biotas may also serve as a framework for conservation actions (for discussion, see Williams et al., 1999). For example, biome identification forms a significant component of the identification of Important Bird Areas, which are considered an important part of the conservation panoply (e.g., Barnes,

1998). In southern Africa, delineation of the Cape Floristic Region as a highly significant biogeographic unit has been instrumental in drawing attention to conservation threats facing the biota in the region (e.g., Cowling, 1992; Richardson et al., 1996).

CONCEPTS AND DEFINITIONS

A wide range of definitions and terms, often scale dependant, are used in the literature to describe areas of environmental transition (termed ecotones). Related terms used in the literature include boundary regions, borders, meeting zones, ecoclines, transitional zones, tension zones, zones of intermingling, and zones of transgression (see Kent et al., 1997, for more on terminology). Below we give a collection of definitions used for the term "ecotone".

Ecotone definitions. "A narrow ecological zone which possesses a mixture of the floristic and faunistic characteristics in between two different and relatively homogenous ecological community types…" (Allen and Starr, 1982).

"…zones where spatial or temporal rates of change in ecological structure or function are rapid relative to rates across the landscape as a whole." (di Castri et al., 1988).

"…transitional areas between adjacent ecological systems, between types of vegetation…areas of steep gradients between the more homogenous [vegetation] associations." (Risser, 1995a).

"…a zone of relatively rapid change between two plant communities and a dynamic zone of interaction which, as a consequence, is often unstable." (Kent et al., 1997).

"Frequently, conditions and the organisms adapted to them change gradually along the gradient, but often there are points of abrupt change, known as ecotones, as, for example, prairie–forest junctions or intertidal zones on a seacoast. An ecotone is not simply a boundary or an edge; the concept assumes the existence of active interaction between two or more ecosystems (or patches of ecosystems), which result in the ecotone having properties that do not exist in either of the adjacent ecosystems …" (Odum, 1997).

In sum, ecotones have been defined as areas of steep transition between communities, ecosystems, or biotic regions. The emphasis is often on the abruptness of the change, which occurs over short geographical distances relative to the spatial extent occupied by the neighboring regions that coincide at these ecotonal areas. Based on these, we suggest that ecotones can be defined as areas of steep environmental transition along an environmental gradient, where the environment rapidly shifts from one type to another based on abiotic (e.g., climatic) and/or biotic factors.

A related research area on which a substantial body of work has focused is that of edge effects. Odum suggested that: "The tendency for increased variety and density at community junctions is known as the *edge effect"* (Odum, 1953) and "Sometimes ecotones are populated by more kinds and larger numbers of birds and game animals than can be found in the interior of the adjoining, more homogeneous communities. Wildlife managers speak of this as the edge effect…" (Odum, 1997). Many studies of the edge effect focus on the local scale, thus making this a special case in the study of ecotones and boundaries.

ECOTONE AND BOUNDARY DETECTION

Determining the exact location of ecotones at multiple scales and quantifying their characteristics pose several challenges. These include spatial detection of the location of ecotones at a given point in time, their temporal dynamics (Noble, 1993; Allen and Breshears, 1998), and their size, shape, sharpness, and other landscape characteristics (Fortin et al., 2000). Diverse tools have been used to detect and quantify boundaries, some of which are described below. Novel tools developed in recent years with the refinement of Geographic Information Systems (GIS), remote sensing, and statistical tools enable us to better quantify and analyze ecotones (Metzger and Muller, 1996; Fortin et al., 2000; Shoshany, 2000). Fortin et al. (2000) and Kent et al. (1997) provide timely reviews of various aspects related to the detection of boundaries, mainly quantitative and methodological issues. This area undoubtedly deserves more theoretical, quantitative, and applied work.

*Methods for detecting and quantifying boundaries.*The study of ecotones consists of two major approaches that focus on examining (i) the gradients in the underlying environmental variables and (ii) the response of populations, species, and communities to these gradients and ecotones. Diverse approaches for the quantification of the steepness of gradients exist. For example, early delineations of biogeographic regions and the ecotonal areas between them were generally based on qualitative assessments (see Hengeveld, 1990, for review), and these continue to form an important component of biogeographic debate. However, the recent advancements of numerical methods such as tools for spatial analysis (e.g., GIS and remote sensing (RS); Schott, 1997; Kerr and Ostrovsky, 2003; Turner et al., 2003) are enabling us to deal more quantitatively with the complexity of boundary regions and ecotones (Fortin et al., 2000).

Two spatial models are applied in GIS for describing the real world, vector (point, line, or polygon features) and raster (x–y grid based). The vector model is useful for describing human landscapes, where boundaries are often linear. However, natural systems and their boundaries are often more complex, as there are rarely clear lines defining their edges. As such, they are better described using continuous variables (e.g., percentage of vegetation cover). The vector model allows calculation of areas, lengths, and fractal dimensions (Fortin et al., 2000), and the analysis of spatial relationships between features. However, the results of these analyses are influenced by the prior definition of the polygons themselves. The application of vector-based GIS tools in landscape ecology may have contributed to boundary regions being ignored, appearing as a one-dimensional line on the map, with emphasis given to the comparison between units defined as more homogenous (e.g., distinct vegetation communities or ecoregions).

The grid-based raster model often allows a more realistic description of continuous variables and of boundaries in natural systems and has been used in many recent conservation-related studies. It can be applied over multiple spatial scales. Each grid cell is given a different value so that the location of ecotones and steepness of gradients can be more readily mapped and analyzed (but see Metzger and Muller, 1996).

Methods for measuring and characterizing ecotones depend on the data available

(e.g., grid or transect, quantitative or qualitative), and include edge detection algorithms and kernels followed by grid data thresholding, or examination of the magnitude of the first and second derivatives for transect data (see below and Fig. 2) (Johnston, 1992; Pitas, 1993; Fortin, 1997; Kent et al., 1997; Fortin et al., 2000; Jacquez et al., 2000; Fagan et al., 2003). Similar techniques are known in the biological sciences as "wombling", after Womble (1951), who proposed a simple method for evaluating the rate of change along a gradient using the first derivative, a method that can be applied for several variables simultaneously by averaging the absolute value of the derivatives, as shown in eq 1.

$$Ef = \frac{\sum_{i=1}^{n} \omega_i \left| \dfrac{\Delta x_i}{\Delta d_i} \right|}{\sum_{i=1}^{n} \omega_i} \tag{1}$$

where Ef is the ecotone detection function, ω_i is the weight assigned to the variable i, and Δx_i is the change in the values of the variable i between two points along a cline, where Δd_i is the distance between them in space.

Moving window techniques (also termed filters in remote sensing (RS), in which the value of a focal grid cell is determined according to its immediate neighboring cells, have also been used to quantify ecotones (Johnston, 1992). The moving split window method (van der Maarel, 1976) enables one to detect those regions where the variance of neighboring samples along a gradient is highest. The basic idea is to detect edges by finding the areas with the highest rate of change among adjacent pixels. The spatial resolution has much effect on the findings. Low-pass filters are designed to smooth noises that confound the detection of sharp gradients and boundaries, while high-pass filters enhance differences between adjacent cells. A combination of both types of filters is recommended, especially when combining data sources of different spatial resolution. Derivatives are an example of such high-pass filters: The first derivative gives the rate of the change on a spatial basis (Johnston, 1992), while the second derivative maps out those regions where the maximum change occurs. Figure 2 presents an example of the use of derivatives to locate and quantify gradient steepness and ecotones along an elevation and the Normalized Difference Vegetation Index (NDVI) profile (Broge and Leblanc, 2000; Kerr and Ostrovsky, 2003).

Whereas most GIS and remote sensing software (e.g., ArcGIS, Erdas, and Idrisi) provide tools for quantifying spatial gradients or for edge detecting, these are usually focused on raster data and do not include statistical tests for the significance of the detected boundary, sub-boundary, or the overlap between the boundaries of various variables (Jacquex et al., 2000). Specific software packages for the analysis of boundary regions have become available recently (e.g., the commercial BoundarySeer software, developed by BioMedware: http://www.terraseer.com/products/boundaryseer.html), enabling a more widespread use of statistical tools for the study of ecotones (e.g., Jacquez and Greiling, 2003; Lu and Carlin, 2005).

An important data source for quantitative ecotone mapping is that of satellite images.
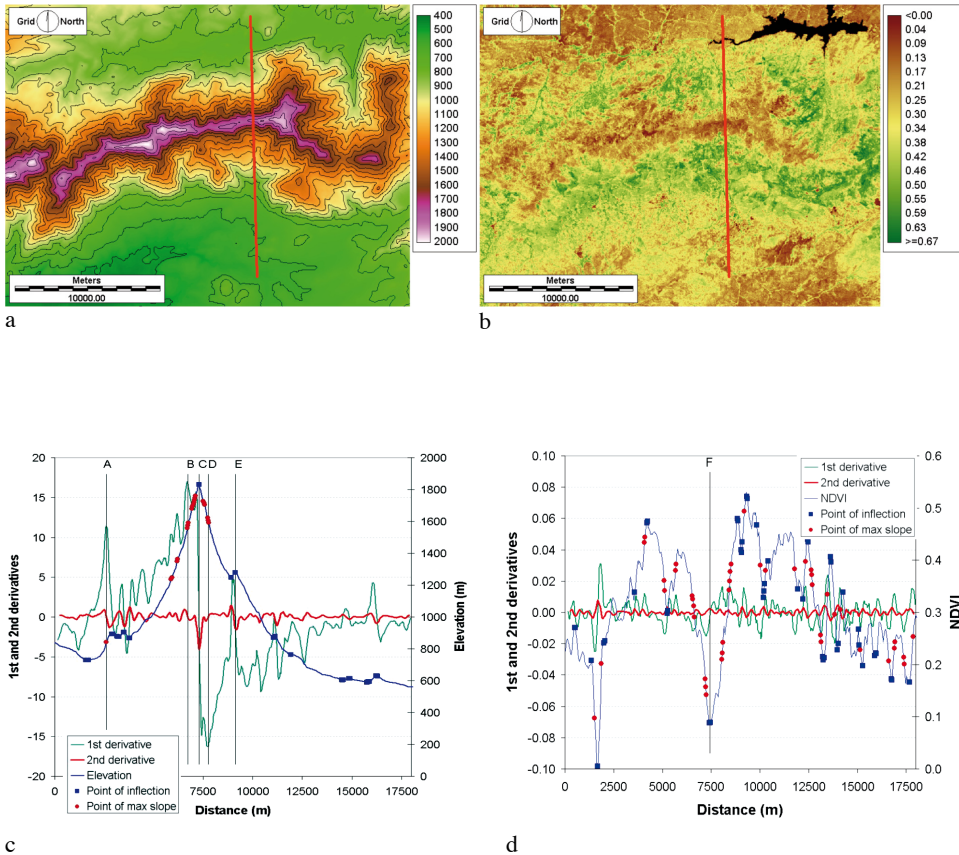
Fig. 2. Quantification of ecotones using derivatives. Example of an analysis showing a proposed approach for analyzing ecotones and gradient steepness based on elevation and the Normalized Difference Vegetation Index (NDVI) along a profile line (shown in red) in a model mountain. A similar approach can be used for other variables and in two dimensions. 2a shows a digital elevation model (DEM). 2b is the NDVI map of the same region. In 2c and 2d we calculated the first and second derivatives (high-pass filters), quantifying the gradient steepness for elevation (2c) and for the NDVI (2d) (along the bold red transect marked in Figs. 2a and 2b). Points of inflection along the transect (e.g., C and E, F marked in blue squares) are points where the first derivative is close to zero, and the second derivative exceeds a user's threshold (depending on the sharpness of the ecotones one is searching for). The ecotones are centered at the points of maximum slope (e.g., A, B and D, marked in red circles), where the first derivative exceeds a user-defined threshold and the second derivative is close to zero (e.g., in 2c the threshold for DEM was 10 for the 1st derivative and 1.3 for the 2nd derivative). The Elevation profile was drawn along the *SIERRADEM* DEM and NDVI files supplied with Idrisi 14.0 software (Clark Labs, 2002).

These images are currently available across multiple spatial scales and resolutions. These span from a few meters to several thousand kilometers (Turner et al., 2003). They offer global monitoring in space and time since the early 1960s for a range of data types (Bowersox and Brown, 2001), including vegetation indices (e.g., NDVI), soil color indices (Mathieu et al., 1998), sea surface temperature (Ohring and Gruber, 2001), digital elevation models, and many others (Kerr and Ostrovsky, 2003). Future work applying RS tools and using additional data types will likely lead to advancements in the study of ecotones and boundary regions.

Beta diversity and additional estimates. In recent years, new approaches to quantifying changes in diversity across boundary areas have been developed and applied. For example, Gaston et al. (2001) used a range of approaches to reflect the location of ecotones based on diversity variation. These include examining whether the values from groups of randomly selected cells (following a grid-based approach) differ significantly when compared with the value of a group of selected cells representing complementary sets; using a measure for biome heterogeneity applying Simpson's index of diversity (see Gaston et al., 2001): $1 - Sum(p_i)^2$ where p_i is the fraction of the grid cell's area occupied by biome i (sensu Krebs, 1999); counting the number of vegetation types in each cell; examining species composition heterogeneity within a certain group (birds, in their case) by calculating the average dissimilarity between each cell and its neighboring cells (also following Krebs, 1999); and an estimate of beta diversity (β_g) that examines rates of species replacement over multidirectional gradients (see Gaston et al., 2001, for more details). A range of beta-diversity estimates can be used for estimating species turnover patterns in space (see Wilson and Shmida, 1984; Lennon et al., 2001; Crist et al., 2003; Koleff et al., 2003, for overviews) and can be applied for (i) determining ecotone locations for a given taxonomic group to be compared with other groups, (ii) comparing patterns of change across spatial scales, (iii) comparing with patterns of richness (alpha diversity), and (iv) setting conservation priorities (Araújo and Williams, 2001). The two most commonly used beta-diversity measures are β_g and β_{sim}, each of which has different properties (Gaston et al., 2001; Lennon et al., 2001; van Rensburg et al., 2004). That is, β_g is a measure of turnover that is primarily a result of differences in species richness, whereas β_{sim} is far more responsive to species compositional differences between neighboring cells (Lennon et al., 2001).

To determine gradients and areas of transition in climatic values (e.g., precipitation and temperature), van Rensburg et al. (2004) calculated the degree of climatic heterogeneity in a raster system for each grid cell compared to its first-order neighboring cells (following a grid-based approach) using the S-PLUS 2000 for ArcView extension (ESRI Inc., 1998). From this, an indicator of spatial association, namely, local Moran's *I* values, was derived for each cell. Following Reyers et al. (2002), the Moran's *I* values were used as the coefficient of autocorrelation. A positive Moran's *I* value represents positive spatial autocorrelation indicating a spatial clustering of similar climatic values. Areas with high positive values of spatial autocorrelation for a given climatic variable can therefore be interpreted as areas with similar climatic conditions along a gradient,

i.e., no major climatic changes. While different studies have used various approaches, we would suggest that future work focusing on comparing the strengths and weaknesses of the different methods could be useful. This work can benefit from consulting with other areas of research, e.g., remote sensing and image analysis, where large advances in boundary detection and gradient quantification methods have been made. Images in these areas range over various scales, from satellite-derived data currently available at a resolution of 0.5 m to 100 km to electron microscope data.

ECOLOGICAL PROCESSES IN ECOTONES

Are ecotones diversity hotspots or marginal sinks? Odum (1953) predicted increased species richness and abundance in ecotones, proposing: "The ecotonal community commonly contains many of the organisms which are characteristic of and often restricted to the ecotone." Often, both the number of species and the population density of some of the species are greater in the ecotone than in the communities flanking it. Table 1 shows several recent studies that support the notion that natural ecotones, at least in some cases, hold especially high diversity at various levels and spatial scales. At the within-species level, several studies found evidence for morphological divergence (between neighboring populations in the ecotone), possibly leading to sympatric speciation in ecotonal regions (Smith et al., 1997), while others point to peak genetic and morphological diversity in ecotone regions. Populations in these regions also harbor unique and rare alleles not found elsewhere (Kark et al., 1999, 2002). At the community level, there is some evidence for high species richness in boundary regions (e.g., Rusek, 1992; Zalewski et al., 2001a,b; Spector, 2002). Kemp and colleagues, in a study on ecotonal diversity at the regional scale that examined reef fish diversity in the Gulf of Aden, found high diversity in the ecotone harboring a unique mixing of three distinct faunas of Oman, the Red Sea, and the Indian Ocean (Kemp, 2000a; Kemp and Benzoni, 2000). This provides evidence that patterns detected in terrestrial ecotones may also occur in the marine realm. Recent work is providing increasing evidence that boundary regions between ecological communities can be highly diverse at both the within-species and the community levels, combining the biological diversity of the adjoining regions and also sustaining unique and rare morphs, genotypes, and species not found elsewhere (Table 1). However, although this pattern has been found to be true in various cases, results vary among studies and can therefore not be generalized, as shown in Table 1.

Why might ecotonal regions show higher species diversity than those in adjacent areas? The answer to this question may help determine whether ecotones deserve special conservation attention. A simple reasoning for such an elevated pattern is the fact that ecotones (by definition) comprise meeting areas between adjoining communities and therefore include a combination of species from two or more community types (Odum, 1971; Risser, 1995a). Such a meeting therefore increases the number of discrete habitats found in the region, causing mass effects due to the dispersal of species into the ecotone region from their respective discrete habitats (Nekola and White, 1999). In other words, the mass effect has been defined as the flow of individuals from areas of high success

Table 1

Results of studies examining biodiversity across ecotones. A wide range of case studies focusing on different goals, groups, regions, ecotone types, and spatial scale of the ecotone have approached the question of whether richness, abundance, and diversity are higher in the ecotone, and whether there are unique ecotonal species. Some of these are summarized in this table. Though this is not an exhaustive review of all studies in the field, results, as seen below, sorted by spatial scale of the ecotone studied, are mixed. In many cases, results point to higher diversity as the ecotone is approached. The table refers mainly to naturally occurring ecotones, though studies that focused on human-generated or experimentally-generated ecotones were also included

Region	Environment/ Ecotone type	Group	Total length of gradient included in the study	Number of sampling points along a transect	Parameters studied	Relative value of parameter in ecotone +: higher 0 : no effect or intermediate – : lower	Reference
Central Bohemia, Czechoslovakia	Grassland–spruce forest ecotone	Soil organisms	Two scales were studied: 50 cm and 24 m	50 and 24	In both scales: Species richness Density Biomass	+ + +	Rusek, 1992
Southwestern New Zealand	Four types of ecotones: native shrubland–forest; forest–mire; old sand dune with exotic pasture–sand dune slack; mown exotic lawn–plantation	Vascular plants	7–40 m*	15–20 per transect	Ecotonal species Species richness	0/+** 0	Lloyd et al., 2000
Hertfordshire, England	Grassland experimental plots (fertilization)	Plants	10 m	37	Species richness	+	Kunin, 1998

Location	Ecotone	Taxon	Width	Number	Measure	Result	Reference
Spain	Gradient from Mediterranean macchia to pine stand within it	Soil nematodes	~25 m	7	Ecotonal species	+	Imaz et al., 2002
Bashkorto-stan, Russia	Xerotermic linden–maple forest–margin to herb–feather grass steppe ecotone	Vascular plants	28 m	14	Species richness Similarity	0 +	Kucherova and Mirkin, 2001
Southern California, USA	Tidal marsh–coastal sage scrub ecotone between the wetland and the upland	Box thorn *Lycium californicum*	11–38 m 149–279 m	All individual plants were mapped	Ecotonal species occurrence	+	James and Zedler, 2000
Kwazulu-Natal, South Africa	Indigenous riparian and exotic pine plantation edges	Birds	Dozens of meters		Ecotonal species Species richness Abundance Diversity	+ 0 0 0	Malan, 2001
Santa Cruz, Bolivia	Sharp tropical evergreen forest–savanna ecotone	Dung beetles (Scarabaei-dae)	100 m	3	Species richness Abundance Biomass	– – –	Spector and Ayzama, 2003
Central Finland	Boreal forest fragments, their edges, and adjacent clearcuts	Carabid beetles	120 m	9	Ecotonal species	0	Heliola et al., 2001
Southeastern Australia	Natural heath-wood ecotone	Birds	250 m	6	Community com-position Ecotonal species	0 0/+***	Baker et al., 2002

continued next page

Table 1—continued

Region	Environment/ Ecotone type	Group	Total length of gradient included in the study	Number of sampling points along a transect	Parameters studied	Relative value of parameter in ecotone +: higher 0 : no effect or intermediate – : lower	Reference
Northwestern Ontario, Canada	Ecotones between coniferous and deciduous forest and between coniferous forest and cutover	Red-backed voles *Clethrionomys gapperi*	390 m	39	Density	0	Kingston and Morris, 2000
New South Wales, Australia	Edge between a riparian habitat on fluvial sands and a saltbush habitat on a stony gibber plain in semi-arid region	Beetles, ants, wasps, flies, and springtails	1,000 m	30	Species richness Abundance	0 0	Dangerfield et al., 2003
Mount Hermon, Israel	Montane elevation gradient	Plants	2,500 m of elevation (over ~15 km)	26	Species richness (Mass effect)	+	Shmida and Wilson, 1985
Judean Desert, Israel	Chaparral–semidesert–desert elevation gradient	Plants	1,300 m of elevation (over 35 km)	14	Species richness (mass effect)	+	Shmida and Wilson, 1985
Northeastern China	Ecotone between eastern forests, meadow grasslands and steppes	Plants			Species richness Life form diversity Life form richness	+/0**** +/0 +/0	Wang et al., 2002

Region	Gradient	Taxa	Extent	n	Variable		Reference
Mount Kinabalu, Sabah, Malaysia	Elevational gradient, ecotone between highland and lowland forest	Small mammals (non-volant), Vegetation	2,500 m of elevation (traps); 3,200 m of elevation (mammal and vegetation data)	6; 33—mammals, 16—vegetation	Mammal species richness; Vegetation species richness	+; +	Md. Nor, 2001
Israel	Mediterranean to arid gradient	Chukar partridge *Alectoris chukar*	~400 km	13	Genetic diversity (allozyme); Morphological diversity; Rare alleles	+; +; +	Kark et al., 1999; 2002
Cameroon	Savannah–rainforest gradient	Birds	~400 km	12	Morphological divergence	+	Smith et al., 1997
Europe (excluding islands)	Continental grid	Rodents	427 squares of ~160 × 160 km		Species density	+	Krystufek and Griffiths, 2002
New World	Ecoregions	Birds	Continent	4889 one-degree grid squares	Species richness; Range size rarity	+; +	Kark et al., 2006

*Scale changed between different ecotones studied: native shrubland–forest — 15 quadrats with 2-m intervals among them; forest-mire — 20 quadrats with 2-m intervals; old sand dune with exotic pasture–sand dune slack — 15 quadrats with 1-m intervals; mown exotic lawn-plantation — 18 quadrats with 0.4-m intervals.

**Ecotonal species were found in all four ecotones using one criterion (presence) and in two of the ecotones using a second criterion (frequency). They were most common in the pasture–sand dune slack and in the mown lawn-plantation ecotones.

***11 of 31 categorized species were ecotone-conspicuous, though none was entirely ecotonal.

****Species numbers, life form richness, and life form diversity were higher in the ecotone and in the eastern forests and lower in the meadow grasslands and typical steppes.

to unfavorable areas (Shmida and Wilson, 1985). This effect results in individuals becoming established in sites where they cannot maintain viable populations, being sinks to larger source populations (Shmida and Wilson, 1985). Consequently, some of these species may reach the edges of their distribution range at the ecotone (comprised of peripheral populations; see Lesica and Allendorf, 1995, for further discussion). These sinks are sustained by constant migration of individuals from more favorable environments, and are expected to have negative net population growth rates. Some evidence for the existence of mass effects can be found in the literature, yet these effects seem to be rather weak, and it is currently unclear whether they can indeed act as a major factor generating high diversity in boundary regions (Kunin, 1998). The mass effect, however, does not predict the occurrence of unique or endemic ecotonal species.

Thus, an open question that remains is whether the ecotone indeed holds unique "ecotonal" species (Odum, 1953, 1997). Odum (1953) proposed that "the transition zone often supports a community with characteristics additional to those of the communities which adjoin the ecotone. Thus…some niches, and therefore, some organisms are likely to be found in the region of the overlap which are not present in either community alone." However, Odum emphasized that "…an increase in density in ecotones is by no means a universal phenomenon." Again, studies testing these predictions show mixed results, some pointing towards the occurrence of ecotonal species, while others do not find evidence for species unique to or highly abundant in ecotones (see Table 1). Currently, it remains unclear whether inconsistency among studies is due to the fact that different species, systems, scales, and regions were used in different studies, or due to methodological factors, such as sampling and analysis approaches. A comparative study of terrestrial and marine systems across spatial scales may provide important insights into the generality of patterns of richness, abundance, and uniqueness in ecotones compared to neighboring environments.

Uniqueness could also be measured based on genetic variability and the appearance of unique alleles, and effective species conservation also depends upon protecting the genetic variability present throughout the range of a species. Whether ecotone populations will have unique genetic structures may largely depend upon whether they serve as peripheral, in additional to ecotonal, populations for a given species. Several studies suggest that peripheral populations (found at the edge of a species distribution) are active regions of speciation (e.g., Levin, 1993) and may therefore hold unique genetic structures that are valuable for conservation (Lesica and Allendorf, 1995; Kark et al., 1999, 2004). Such uniqueness, however, depends on the degree of genetic drift and intensity of natural selection pressures to which a given periphery population has been exposed (Lesica and Allendorf, 1995). Therefore, to assess the extent to which ecotones support a community with characteristics additional to those of the communities adjacent to the ecotone, it is important to evaluate the genetic diversity of the ecotonal population compared to the adjoining regions.

ECOTONES AND EVOLUTIONARY PROCESSES

Work focusing on evolutionary processes has suggested that ecotones may serve as centers of evolutionary novelty that maintain evolutionary processes, where parapatric

(or sympatric) speciation processes may take place (Schilthuizen, 2000). Support for this comes from recent research at the genetic and phenotypic levels (Smith et al., 1997; Schneider et al., 1999; Schilthuizen, 2000; Kark et al., 2002), as reviewed in Moritz et al., 2000. If boundary regions harbor, at least in some cases, unique and endemic species and alleles, this may provide support for the notion that these regions also serve as centers of speciation. If this is the case, ecotonal regions are expected to contain a preponderance of recently derived species that are yet to expand their ranges (neo-endemics) (Mora et al., 2003). Fjeldså and Rahbek (1998) suggested that indeed more recently evolved species were concentrated in transitional ecotones surrounding the main central African rainforest. Moritz and colleagues (Moritz et al., 2000) further proposed that areas such as the central African ecotones hold concentrations of young species and evolutionary novelty, and are important for maintaining the evolutionary processes. This reasoning is congruent with the finding that terrestrial ecotones sustain high morphological divergence, providing evidence that current speciation processes may be taking place in these regions (Smith et al., 1997; Moritz et al., 2000; Schilthuizen, 2000). This suggests that ecotonal regions may be valuable for the maintenance of evolutionary processes (Smith et al., 1997; Moritz et al., 2000). If indeed areas of transition maintain and even generate biological diversity, serving as speciation pumps, then they should receive higher priority rather than simply being defined as marginal areas in which diversity maintenance and processes depend on other areas. Steep gradients and ecotonal areas have been shown to serve as sources for sympatric speciation (e.g., Schneider et al., 1999), as well as allopatric speciation that occurs in peripheral areas of the range (Mayr, 1970) that often corresponds with ecotones.

The importance of ecological and evolutionary processes in shaping biodiversity patterns and processes in ecotones is expected to differ among spatial scales. For example, at local scales, population processes and metapopulation dynamics as well as competition and predation may play a major role, while evolutionary processes such as speciation and extinction will tend to be more important at global and continental scales. Studies examining the role of ecological vs. evolutionary processes in shaping biodiversity in ecotones are likely to be a useful direction. The difference in views between those suggesting that ecotones should receive high conservation priority (e.g., Smith et al., 1997, 2001) and those suggesting that these areas are dependent on other parts of the range and therefore should not receive special attention may partly depend on whether ecological or evolutionary processes are examined, as well as on the scale addressed.

BOUNDARIES AND HYBRID ZONES

"At the confluence of two or more genetic streams, with chromosomes constantly 'crossing over', this mixture of races, rather than resulting in an inferior being, provides hybrid progeny, a mutable, more alleable species with a rich gene pool. From this racial, ideological, cultural and biological cross-pollenization, an 'alien' consciousness is presently in the making—a new mestiza consciousness, una conciencia de mujer. It is a consciousness of the Borderlands" *(Anzaldúa, 1987)*.

Are ecotones and sharp environmental gradients congruent with hybrid zones? Rather

limited work has directly addressed this question or tried to quantify the relationship between the location of hybrid zones and that of ecotones between ecological communities based on multiple taxa and regions. Hybrid zones are defined as regions where genetically distinct geographical populations meet and mate, resulting in individuals of mixed ancestry (Jiggins and Mallet, 2000) and geographical region(s) where differentiated populations interbreed (Freeman and Herron, 2001). Using species distribution atlases of African birds, Endler (1982) estimated that 52% of the contact zones between sister species occur between forest and savannah (see also Moritz et al., 2000). Schilthuizen and Lombaerts (1995) found correspondence between the abruptness of an ecological transition and hybrid zones. Working on angelfish (*Pomacanthus*) in the Gulf of Aden, Kemp (2000b) found that the ecotone was the location of hybridization between *Pomacanthus maculosus* and *P. semicirculatus*. Whitham et al. (1999) suggested that plant hybrid zones tend to be biodiversity centers with high species richness and abundance and may provide essential habitats for rare species. Interspecific hybridization can lead to hybrid zones that have high genetic variation (Whitham et al., 1999). Populations in these regions have unique additional diversity to that of the hybridizing species, which can also affect an associated complex ecological community (Hewitt, 2000). For example, both invertebrates and vertebrates respond to hybrid plants. If these are concentrated in zones where many species form hybrids, they may translate to a larger community effect (Whitham et al., 1999). Thus at least some predictions for ecotones and hybrid zones appear to be congruent, and it may prove valuable to examine their separate and combined effects in speciation processes and in shaping biodiversity patterns. This could be done, for example, by comparing ecotones that overlap in space with hybrid zones with those that do not.

HUMAN-RELATED BOUNDARIES

While natural environmental factors such as soils, geology, and sharp rainfall gradients may generate ecotones, sharp transitions may also result from human-related factors such as land use changes, agriculture, grazing, or burning (Kent et al., 1997). Consequently, a valid question to ask is what influences do landscape transformation and human population size have on species biogeographic patterns? van Rensburg et al. (2004) addressed this question across South Africa and found that, at least at the quarter-degree resolution, biogeographic patterns in birds can be recovered using modern data despite landscape transformation. However, it is likely that the resolution of the study was too coarse to reveal finer-scale effects. That is, human-related boundaries, too, may occur at multiple spatial scales, ranging from very local boundaries between agricultural plots, urban areas, roads, and the neighboring native habitat to large-scale human-related ecotones, such as shifting desert borders due to desertification processes. These boundaries may be either static and fixed or dynamic and shifting. Current human activity is generating boundaries that did not exist before, is changing their steepness, and is shifting their location.

While the early ecotone literature dealt mainly with natural boundaries, recent work includes both natural and human-caused boundaries (Foggo et al., 2001). Human-related

boundaries have been proposed as potentially being sharper than natural ones. Kent et al. (1997) suggested that "the sharpest ecotones are often created or maintained by human activity." Odum (1953) argued that "in fact, it seems likely that ecotones assume greater importance where man has greatly modified natural communities, so that the patchwork of small community areas and numerous ecotones result. Species which may originally have been characteristic of large tracts must either become adapted to ecotones or become extinct". Methods for studying natural vs. human-related boundaries can be different, and we expect that this area will receive increasing attention in future studies, with the advancement of the study of urban ecology and biodiversity in human-dominated landscapes.

ECOTONES, GLOBAL CHANGE, AND CONSERVATION APPLICATIONS

Substantial conservation attention has been given in recent years to the understanding and mapping of biodiversity patterns, and the underlying processes. Predicting the effects of global change (e.g., climate change, biological invasions, and habitat loss) on natural populations has become more clear. As noted above, there has been an interesting discussion in the literature in recent years regarding whether transitional areas are valuable for conservation (e.g., Smith et al., 2001, vs. Brooks et al., 2001). In our opinion, ecotone and boundary regions, where change, shifts, and variability occur naturally in both space and time, could serve as useful models for understanding, monitoring, and predicting the response of individuals, populations, and communities to changing environments. This is especially relevant as climate shifts are expected to be rapid and extreme in boundary regions between ecosystems (Allen and Breshears, 1998). Boundary regions can provide important insights into the processes that generate and maintain diversity and novelty (Schilthuizen, 2000; Smith et al., 2001), which are crucial in the face of current declines of populations and losses of genetically distinct populations within species, and entire species resulting from global change. Ecotonal areas can therefore potentially serve as "early warning" indicators or detectors of global climate changes through the tracking of changes in ecotone locations over time. However, this response depends on the spatial and temporal scales examined and may be a more useful indicator at global spatial scales and rather coarse time scales, and therefore deserves further work due to the complexity of the factors affecting the location of ecotones in space and time (Kupfer and Cairns, 1996; Holtmeier and Broll, 2005; but see Noble, 1993).

Recent years have been characterized by an intensive search for diversity-rich hotspots, areas with especially high species richness and endemism (e.g., Myers et al., 2000). Much recent focus has centered on prioritizing conservation efforts across different ecoregions, biomes, and ecological communities (Olson and Dinerstein, 1998). In this search for biodiversity hotspots, boundary regions between ecological regions have largely been ignored, especially in large-scale analyses (Smith et al., 2001). This is surprising since areas of transition and biogeographic crossroads often provide conservation strategists with opportunities to simultaneously conserve high species richness and zones of high beta diversity and complementarity (Araújo and Williams, 2001; Spector, 2002, but see Gaston et al., 2001, for potential conservation concerns regarding

complementarity), as well as evolutionary processes (Schilthuizen, 2000). If ecotonal areas indeed maintain and generate especially high richness as well as unique and novel species and forms, they deserve far greater conservation and research attention than they are currently receiving (Smith et al., 2001) (see suggestions for future research below). Due to their small sizes, this may also be a cost-effective strategy.

Nevertheless, conservation plans for ecotones should not be made independent of their surrounding environments. If ecotone dynamics are at least partly maintained by gene flow, migration, and other interactions with the more homogenous adjacent communities, then their independent conservation may miss the goal. Ecotonal regions are important for our understanding of evolutionary (such as speciation, divergence with gene flow, and adaptation) and ecological processes (e.g., response of populations to fluctuating environments, biodiversity centers). They may enable us to better predict the responses of populations to environmental change and to identify biodiversity hotspots valuable for conservation. Given future uncertainty, preserving these areas may maximize the probability of a viable response of populations and species to changing environments.

FUTURE WORK

The study of ecotones, boundary regions, and areas of transition provides many new avenues for future research. Here we identify some of the most immediate.

- Global change and ecotones: Studies should model and experimentally test the potential response of populations and communities in ecotone regions to global environmental changes, including climatic changes, alien species invasion, and land-use changes. This direction deserves further work in different regions and ecotone types. Questions include: How resistant are ecotone populations to changing environments? Under what conditions are ecotones pathways vs. barricades to biological invasions?
- Patterns and processes shaping diversity across ecotones: What processes generate the patterns in ecotones? What is the relative importance of ecological vs. evolutionary factors? Do patterns show fractal characteristics (Anand and Li, 2001)? Are processes occurring in natural ecotones similar to those in human-generated boundaries?
- Ecotones and metapopulation dynamics: Are ecotonal populations sinks or sources in terms of their metapopulation structure and dynamics? Are populations in these areas dependent on migration and gene flow from neighboring areas, serving as sinks, or are they actually able to maintain themselves over time and serve as sources to other areas?
- Ecotonal species: A meta-analysis bringing together theory and empirical studies can provide useful insights. Questions that require more attention include: Under what conditions are ecotonal species expected to be found? Do ecotonal species have common traits that enable them to persist in boundary regions? Do they belong to taxonomic groups with distinctive characteristics? Are they young species currently

diverging in the ecotone region via parapatric speciation or rather wide-ranging species that have expanded their ranges to ecotonal environments?

- Spatio-temporal heterogeneity and ecotones: An open question is whether variability in space and time is higher in ecotones. If ecotonal regions show higher environmental heterogeneity (Fortin et al., 2000; Zalewski et al., 2001a), this may enable more species and more genotypes to coincide in the ecotone. Another direction that requires more attention is the study of how the ecotone location, its abruptness, width, and other characteristics shift over time, comparing gradual and abrupt shifts, as well as short- and long-term time scales.

- The interaction between ecotones and species ranges: More work is needed that directly examines the relationship between ecotones and the dynamics of species ranges, especially approaching the periphery. This direction has important implications for conservation. If peripheral populations occupy boundaries between communities, then efforts to conserve them may not yield long-term persistence (Araújo and Williams, 2001; Gaston et al., 2001), as these populations are small, isolated, and governed by stochastic demographic processes and genetic drift. On the other hand, if populations found in boundary areas are sub-peripheral, rather than extreme peripheries of species ranges, then ecotonal populations may have greater likelihood of persistence in the face of environmental change (Kark et al., 1999, in press).

- Multiple ecotones: So far, most work has focused on single ecotones; few studies have examined the effects of multiple ecotones and boundaries. Is there an increasing ecotonal effect where multiple regions coincide? This direction has applied conservation implications.

- Methods for studying boundary regions, ecotones, and gradients: More attention needs to be given to sampling, quantification, analysis, and interpretation aspects to enable us to address questions on ecotones and boundary regions at multiple spatial scales (Kent et al., 1997). Research in the field would benefit from collaboration with investigators in spatial statistics, geophysics, mathematics, image processing, computer science, remote sensing, and GIS.

- The role of ecological vs. evolutionary processes in shaping biodiversity in ecotones: Further studies examining the role of processes such as dispersal, extinction, and speciation in shaping diversity patterns in ecotones will likely provide important insight into the importance of spatial scale in shaping ecotonal diversity and in solving some of the disagreement seen in the literature regarding transitional areas.

Answers to these questions and others will enable us to determine the role of ecotones in ecology and evolution and to assign conservation priorities for these areas.

ACKNOWLEDGMENTS

REFERENCES

Allen, C.D., Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences of the United States of America 95: 14839–14842.

Allen, T.F.H., Starr, T.B. 1982. Hierarchy. Perspectives for ecological complexity. University of Chicago Press, Chicago.

Anand, M., Li, B.L. 2001. Spatiotemporal dynamics in a transition zone: patchiness, scale, and an emergent property. Community Ecology 2: 161–169.

Anzaldúa, G. 1987, Borderlands/La Frontera: the New Mestiza. Aunt Lute Books, San Francisco.

Araújo, M.B., Williams, P.H. 2001. The bias of complementarity hotspots toward marginal populations. Conservation Biology 15: 1710–1720.

Baker, J., French, K., Whelan, R.J. 2002. The edge effect and ecotonal species: bird communities across a natural edge in southeastern Australia. Ecology 83: 3048–3059.

Barnes, K.N. 1998. The important bird areas of southern Africa. BirdLife South Africa, Johannesburg.

Bestelmeyer, B.T., Wiens, J.A. 2001. Local and regional-scale responses of ant diversity to a semiarid biome transition. Ecography 24: 381–392.

Boone, R.B., Krohn, W.B. 2000. Relationship between avian range limits and plant transition zones in Maine. Journal of Biogeography 27: 471–482.

Bowersox, M.A., Brown, D.G. 2001. Measuring the abruptness of patchy ecotones: a simulation-based comparison of landscape pattern statistics. Plant Ecology 156: 89–103.

Broge, N.H., Leblanc, E. 2000. Comparing prediction power and stability of broadband and hyperspectral vegetation indices for estimation of green leaf area index and canopy chlorophyll density. Remote Sensing of Environment 76: 156–172.

Brooks, T.M., Hanah, L., da Fonseca, G.A.B., Mittermeier, R.A. 2001. Prioritizing hotspots, representing transitions. Trends in Ecology and Evolution 16: 673.

Clark Labs, 2002. The Idrisi project. Clark Laboratories, Worcester, MA.

Clements, F.E. 1897. Peculiar zonal formations of the Great Plains. American Naturalist 31: 968–970.

Clements, F.E. 1905. Research methods in ecology. University of Nebraska Publishing Company, Lincoln, NB.

Cowling, R.M. 1992. The ecology of Fynbos. Nutrients, fire and diversity. Oxford University Press, Cape Town.

Cox, C.B. 2001. The biogeographic regions reconsidered. Journal of Biogeography 28: 511–523.

Crist, T.O., Veech, J.A., Gering, J.C., Summerville, K.S. 2003. Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β, and γ diversity. The American Naturalist 162: 734–743.

Curtis, J.T. 1959. The vegetation of Wisconsin: an ordination of plant communities. University of Wisconsin Press, Madison, WI.

Dangerfield, J.M., Pik, A.J., Britton, D., Holmes, A., Gillings, M., Oliver, I., Briscoe, D., Beattie, A.J. 2003. Patterns of invertebrate biodiversity across a natural edge. Austral Ecology 28: 227–236.

Darlington, P.J. 1957. Zoogeography: the geographical distribution of animals. John Wiley, New York.

di Castri, F., Hansen, A.J., Holland, M.M. 1988. A new look at ecotones—emerging international

projects on landscape boundaries. International Union of Biological Sciences, Paris.

Endler, J.A. 1982. Pleistocene forest refuges: fact or fancy. In: Prance, G.T., ed. Biological diversification in the tropics. Columbia University Press, New York.

ESRI Inc. 1998. Environmental Systems Research Institute, Inc., Redlands, CA.

Fagan, W.F., Fortin, M.-J., Soykan, C. 2003. Integrating edge detection and dynamic modeling in quantitative analyses of ecological boundaries. BioScience 53 (8): 730–738.

Fjeldså J., Rahbek, C. 1998. Continent-wide conservation priorties and diversification processes. In: Mace, G., Balmford, A., Ginsberg, J., eds. Conservation in a changing world. Cambridge University Press, Cambridge, pp. 107–138.

Foggo, A., Ozanne, C.M.P., Speight, M.R., Hambler, C. 2001. Edge effects and tropical forest canopy invertebrates. Plant Ecology 153: 347–359.

Fortin, M.-J. 1997. Effects of data types on vegetation boundary delineation. Canadian Journal of Forest Research 27: 1851–1858.

Fortin, M.-J., Olson, R.J., Ferson, S., Iverson, L., Hunsaker, C., Edwards, G., Levine, D., Butera, K., Klemas, V. 2000. Issues related to the detection of boundaries. Landscape Ecology 15: 453–466.

Freeman, S., Herron, J.C. 2001. Evolutionary analysis, 2nd ed. Prentice Hall, Upper Saddle River, New Jersey.

Gaston, K.J., Rodrigues, A.S.L., van Rensburg, B.J., Koleff, P., Chown, S.L. 2001. Complementary representation and zones of ecological transition. Ecology Letters 4: 4–9.

Gosz, J.R. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hansen, A.J., di Castri, F. eds. Landscape boundaries: consequences for biotic diversity and ecological flows. Ecological Studies, Vol. 92. Springer Verlag, New York, pp. 55–75.

Gosz, J.R. 1993. Ecotone hierarchies. Ecological Applications 3: 369–376.

Gosz, J.R., Sharpe, P.J.H. 1989. Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. Landscape Ecology 3: 229–243.

Heliola, J., Koivula, M., Niemela, J. 2001. Distribution of carabid beetles (Coleoptera, Carabidae) across a boreal forest-clearcut ecotone. Conservation Biology 15: 370–377.

Hengeveld, R. 1990. Dynamic biogeography. Cambridge University Press, Cambridge.

Hewitt, G.M. 2000. The genetic legacy of the Quaternary ice ages. Nature 405: 907–913.

Holland, M., Risser, P., Naiman, R. 1991. Ecotones. Chapman and Hall, New York.

Holtmeier, F.-K., Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. Global Ecology and Biogeography 14: 395–410.

Imaz, A., Hernandez, M.A., Arino, A.H., Armendariz, I., Jordana, R. 2002. Diversity of soil nematodes across a Mediterranean ecotone. Applied Soil Ecology 20: 191–198.

Jacquez, G.M., Greiling, D.A. 2003. Geographic boundaries in breast, lung and colorectal cancers in relation to exposure to air toxics in Long Island, New York. International Journal of Health Geographics 2 (4), doi: 10.1186/1476-072X-2-4

Jacquez, G.M., Maruca S., Fortin, M.-J. 2000. From fields to objects: a review of geographic boundary analysis. Journal of Geographic Systems 2: 221–241.

James, M.L., Zedler, J. 2000. Dynamics of wetland and upland subshrubs at the salt marsh-coastal sage scrub ecotone. American Midland Naturalist 143: 298–311.

Jiggins, C.D., Mallet, J. 2000. Bimodal hybrid zones and speciation. Trends in Ecology and Evolution 15: 250–255.

Johnston, C.A. 1992. Quantitative methods for studying landscape boundaries. In: Hansen, A.J.,

di Castri, F., eds. Landscape boundaries: consequences for biotic diversity and ecological flows. Ecological Studies, Vol. 92. Springer-Verlag, New York, pp. 107–124.

Kark, S., Alkon, P.U., Safriel, U.N., Randi, E. 1999. Conservation priorities for chukar partridge in Israel based on genetic diversity across an ecological gradient. Conservation Biology 13: 542–552.

Kark, S., Mukerji, T., Safriel, U.N., Nissani, R., Darvasi, A. 2002. Peak morphological diversity in an ecotone unveiled in the chukar partridge by a novel Estimator in a Dependent Sample (EDS). Journal of Animal Ecology 71: 1015–1029.

Kark, S., Volis, S., Novoplansky, A. 2004. Biodiversity along core-periphery distribution clines. In: Shachak, J.R., Gosz, J.R., Pickett, S.T.A., Perevoltsky, A., eds. Biodiversity in drylands. Oxford University Press, pp. 30–56.

Kark, S., Allnutt, T.F., Levin, N., Manne, L.L., Williams, P.H. 2006. The role of transitional areas as avian biodiversity centres. Global Ecology and Biogeography (in press, available on-line).

Kemp, J.M. 2000a. Zoogeography of the coral reef fishes of the north-eastern Gulf of Aden, with eight new records of reef fishes from Arabia. Fauna of Arabia 18: 293–321.

Kemp, J.M. 2000b. Hybridisation of the marine angelfishes *Pomacanthus maculosus* and *P. semicirculatus* in the Gulf of Aden. Fauna of Arabia 18: 357–367.

Kemp, J.M., Benzoni, F. 2000. A preliminary study of coral communities of the northern Gulf of Aden. Fauna of Arabia 18: 67–86.

Kent, M., Gill, W.J., Weaver, R.E., Armitage, R.P. 1997. Landscape and plant community boundaries in biogeography. Progress in Physical Geography 21: 315–353.

Kerr, J.T., Ostrovsky, M. 2003. From space to species: ecological applications for remote sensing. Trends in Ecology and Evolution 18: 299–205.

Kingston, S.R., Morris, D.W. 2000. Voles looking for an edge: habitat selection across forest ecotones. Canadian Journal of Zoology-Revue Canadienne de Zoologie 78: 2174–2183.

Koleff, P., Gaston, K.J., Lennon, J.J. 2003. Measuring beta diversity for presence-absence data. Journal of Animal Ecology 72: 367–382.

Krebs, C.J. 1999. Ecological methodology, 2nd ed. Addison-Wesley, Reading, MA.

Krystufek, B., Griffiths, H.I. 2002. Species richness and rarity in European rodents. Ecography 25: 120–128.

Kucherova, S.V., Mirkin, B.M. 2001. On methods for analyzing ecotones of forest margins. Russian Journal of Ecology 32: 310–314.

Kunin, W.E. 1998. Biodiversity at the edge: a test of the importance of spatial "mass effects" in the Rothamsted Park Grass experiments. Proceedings of the National Academy of Sciences of the United States of America 95: 207–212.

Kupfer, J.A., Cairns, D.M. 1996. The suitability of montane ecotones as indicators of global climatic change. Progress in Physical Geography 20: 253–272.

Lennon, J.J., Koleff, P., Greenwood, J.J.D., Gaston, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. Journal of Animal Ecology 70: 966–979.

Leopold, A. 1933. Game management. Charles Scribner's Sons, New York.

Lesica, P., Allendorf, F.W. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9: 753–760.

Levin, D.A. 1993. Local speciation in plants: the rule not the exception. Systematic Botany 18: 197–208.

Lidicker, W.Z.Jr. 1999. Responses of mammals to habitat edges: an overview. Landscape Ecology 14: 333–343.

Livingston, B.E. 1903. The distribution of the upland societies of Kent County, Michigan. Botanical Gazette 35: 36–55.

Lloyd, K.M., McQueen, A.A.M., Lee, B.J., Wilson, R.C.B., Walker, S., Wilson, J.B. 2000. Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. Journal of Vegetation Science 11: 903–910.

Lu, H., Carlin, B.P. 2005. Bayesian areal wombling for geographical boundary analysis. Geographical Analysis 37: 265–285.

Malan, G. 2001. The avifauna of riparian-Pinus habitat edges at Mooiplaas forestry estate, KwaZulu-Natal, South Africa. South African Journal of Wildlife Research 31: 73–84.

Mathieu, R., Pouget, M., Cervelle, B., Escadafal, R. 1998. Relationships between satellite-based radiometric indices simulated using laboratory reflectance data and typic soil color of an arid environment. Remote Sensing of Environment 66: 17–28.

Mayr, E. 1970. Populations, species, and evolution. Belknap Press, Cambridge, MA.

Md. Nor, S. 2001. Elevational diversity patterns of small mammals on Mount Kinabalu, Sabah, Malaysia. Global Ecology and Biogeography 10: 41–62.

Metzger, J.P., Muller, E. 1996. Characterizing the complexity of landscape boundaries by remote sensing. Landscape Ecology 11: 65–77.

Mora, C., Chittaro, P.M., Sale, P.F., Kritzer, J.P., Ludsin, S.A. 2003. Patterns and processes in reef fish diversity. Nature 421: 933–936.

Moritz, C., Patton, J.L., Schneider, C.J., Smith, A.R. 2000. Diversification of rainforest faunas: an integrated molecular approach. Annual Review of Ecology and Systematics 31: 533–563.

Morrone, J.J. 2002. Biogeographical regions under track and cladistic scrutiny. Journal of Biogeography 29: 149–152.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Nekola, J.C., White, P.S. 1999. The distance decay of similarity in biogeography and ecology. Journal of Biogeography 26: 867–878.

Noble, I.R. 1993. A model of the responses of ecotones to climate change. Ecological Applications 3: 396–403.

Odum, E.P. 1953. Fundamentals of ecology. W.B. Saunders, Philadelphia.

Odum, E.P. 1971. Fundamentals of ecology. W.B. Saunders, Philadelphia.

Odum, E.P. 1997. Ecology: a bridge between science and society. Sinauer Associates, Sunderland, MA.

Ohring, G., Gruber, A. 2001. Climate monitoring from operational satellites accomplishments, problems, and prospects. Advances in Space Research 28: 207–219.

Olson, D.M., Dinerstein, E. 1998. The Global 200: a representation approach to conserving the Earth's most biologically valuable ecoregions. Conservation Biology 12: 502–515.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M. 1995. The future of biodiversity. Science 269: 347–350.

Pitas, I. 1993. Digital image processing algorithms. Prentice Hall, New York.

Poynton, J.C. 1961. Biogeography of south-east Africa. Nature 189: 801–803.

Poynton, J.C., Boycott, R.C. 1996. Species turnover between Afromontane and eastern African lowland faunas: patterns shown by amphibians. Journal of Biogeography 23: 669–680.

Reyers, B., Fairbanks, D.H.K., Wessels, K.J., van Jaarsveld, A.S. 2002. A multicriteria approach to reserve selection: addressing long-term biodiversity maintenance. Biodiversity and Conservation 11: 769–793.

Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M., McKell,

D.H. 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. Biodiversity and Conservation 5: 607–647.

Risser, P.G. 1993. Ecotones. Ecological Applications 3: 367–368.

Risser, P.G. 1995a. The status of the science examining ecotones. BioScience 45: 318–325.

Risser, P.G. 1995b. Biodiversity and ecosystem function. Conservation Biology 9: 742–746.

Rusek, J. 1992. Distribution and dynamics of soil organisms across ecotones. In: Hansen, A.J., di-Castri, F., eds. Landscape boundaries: consequences for biotic diversity and ecological flows. Ecological studies, Vol. 92. Springer-Verlag, New York, pp. 196–214.

Schilthuizen, M. 2000. Ecotone: speciation-prone. Trends in Ecology and Evolution 15: 130–131.

Schilthuizen, M., Lombaerts, M. 1995. Life on the edge: a hybrid zone in *Albinaria hippolyti* from Crete. Biological Journal of the Linnean Society 54: 111–138.

Schneider, C.J., Smith, T.B., Larison, B., Moritz, C. 1999. A test of alternative models of diversification in tropical rainforests: ecological gradients vs. rainforest refugia. Proceedings of the National Academy of Sciences of the United States of America 96: 13869–13873.

Schott, J.R. 1997. Remote sensing: the image chain approach. Oxford University Press, New York.

Shmida, A., Wilson, M.V. 1985. Biological determinants of species diversity. Journal of Biogeography 12: 1–20.

Shoshany, M. 2000. Satellite remote sensing of natural Mediterranean vegetation: a review within an ecological context. Progress in Physical Geography 24: 153–178.

Smith, T.B., Wayne, R.K., Girman, D.J., Bruford, M.W. 1997. A role for ecotones in generating rainforest biodiversity. Science 276: 1855–1857.

Smith, T.B., Kark, S., Schneider, C.J., Wayne, R.K., Moritz, C. 2001. Biodiversity hotspots and beyond: the need for conserving environmental transitions. Trends in Ecology and Evolution 16: 431.

Spector, S. 2002. Biogeographic crossroads as priority areas for biodiversity conservation. Conservation Biology 16: 1480–1487.

Spector, S., Ayzama, S. 2003. Rapid turnover and edge effects in dung beetle assemblages (Scarabaeidae) at a Bolivian neotropical forest–Savanna ecotone. Biotropica 35: 394–404.

Srivastava, D. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. Journal of Animal Ecology 68: 1–16.

Turner, W., Spector, S., Gardiner, N., Fladeland, M., Sterling, E., Steininger, M. 2003. Remote sensing for biodiversity science and conservation. Trends in Ecology and Evolution 18: 306–314.

van der Maarel, E. 1976. On the establishment of plant community boundaries. Berichte der Deutsche Botanische Gesellschaft 89: 415–443.

van Rensburg, B.J., Chown, S.L., McGeoch, M.A., van Jaarsveld, A.S. 2000. Spatial variation and biogeography of sand forest avian assemblages in South Africa. Journal of Biogeography 27: 1385–1401.

van Rensburg, B.J., Koleff, P., Gaston, K.J., Chown, S.L. 2004. Spatial congruence of ecological transition at the regional scale in South Africa. Journal of Biogeography 31: 843–854.

Wang, R.Z., Gao, Q., Tang, H.P. 2002. Variations of plant life form diversity along the Northeast China Transect and its direct gradient analysis. Journal of Environmental Sciences-China 14: 547–551.

Whitham, T.G., Martinsen, G.D., Floate, K.D., Dungey, H.S., Potts, B.M., Keim, P. 1999. Plant hybrid zones affect biodiversity: tools for a genetic-based understanding of community struc-

ture. Ecology 80: 416–428.

Williams, P.H. 1996. Mapping variations in the strength and breath of biogeographic transition zones using species turnover. Proceedings of the Royal Society of London B 263: 579–588.

Williams, P.H., de Klerk, H.M., Crow, T.M. 1999. Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. Journal of Biogeography 26: 459–474.

Wilson, M.V., Shmida, A. 1984. Measuring beta diversity with presence-absence data. Journal of Ecology 72: 1055–1064.

Womble, W.H. 1951. Differential systematics. Science 114: 315–322.

Zalewski, M., Schiemer, F., Thorpe, J. 2001a. Fish and land-inland water ecotones: overview and synthesis. Ecohydrology and Hydrobiology 1: 261–266.

Zalewski, M., Thorpe, J.E., Naiman, R.J. 2001b. Fish and riparian ecotones: a hypothesis. Ecohydrology and Hydrobiology 1: 11–24.