



EFFECTS OF ECOTONES ON BIODIVERSITY

Salit Kark

The Hebrew University of Jerusalem

- I. Concepts and Terminology
 - II. Early Work on the Effects of Ecotones on Biodiversity
 - III. The Measurement of Ecotones
 - IV. Patterns of Biodiversity in Ecotones
 - V. Processes Shaping Biodiversity in Ecotones
 - VI. Conclusions
-

storage, retrieval, analysis, and display of spatial (locationally defined) data.

remote sensing The science and art of obtaining information about an object, area, or phenomenon through the analysis of data acquired by a device that is not in contact with the object, area, or phenomenon under investigation (e.g., via a satellite image).

GLOSSARY

beta diversity Also called species turnover, beta diversity refers to the change in species as one moves between habitats, communities, or ecosystems.

divergence-with-gene-flow model of speciation A model explaining the process of species formation (speciation) in which new species diverge in the face of gene flow; the movement of genes within a group that results from mating with immigrant individuals.

ecotone A sharp transition zone between two or more different ecological communities or regions.

ecotone effect The pattern of increased species richness (number of species) and abundance in ecotones and the occurrence of unique ecotonal species.

edge effect The effect of the juxtaposition of contrasting environments on an ecosystem.

geographic information systems (GIS) A computer-based system for creating and managing spatial data and associated attributes. It enables the capture,

ECOTONES are areas of steep transition between ecological communities, ecosystems, or ecological regions along an environmental gradient. Ecotones occur at multiple spatial scales and range from natural boundaries to human-generated ecotones. Various studies have shown that species richness and abundances tend to peak in ecotonal areas, though exceptions to these patterns occur. Recent evidence suggests that ecotones may also be speciation centers. Some researchers suggest that ecotones do not deserve high conservation priority, holding marginal populations. Alternatively, others argue that ecotones deserve special and high conservation investment, potentially serving as speciation and biodiversity centers.

I. CONCEPTS AND TERMINOLOGY

Ecotones are areas where ecological communities, ecosystems, or biotic regions coincide. They often occur in areas of steep environmental transition, along environmental gradients. In these transitional regions,

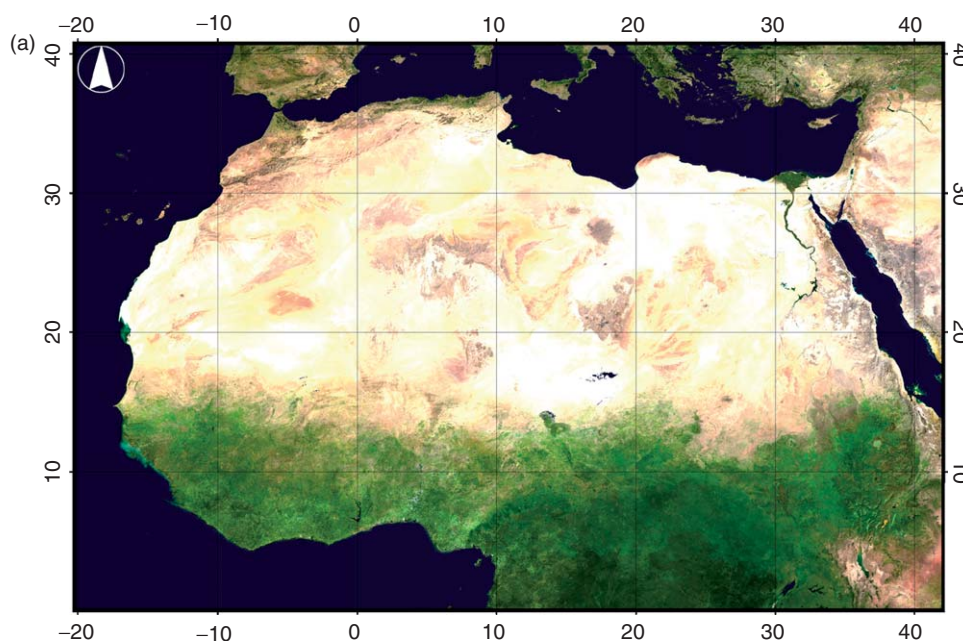


FIGURE 1 Satellite images showing a variety of natural and human-generated ecotones at several spatial scales. (a) Ecotones in the Sahel region of Africa (see text). Source: NASA Blue Marble Next Generation, August 2004. True color composite of MODIS satellite images. (a) From Stöckli *et al.* (2005). Downloaded from Visible Earth (2006). Image by NASA Visible Earth <http://visibleearth.nasa.gov> (b) Altitudinal ecotones between vegetation belts in Mt. Kenya. (c) Natural and human-made ecotones on Hawaii's big island. Ecotones vary over different slopes and elevations. Note also the sharper ecotones in areas where lava has flowed. (d) Human-related ecotones resulting from deforestation (in pink) in the Amazon Basin, Brazil. On the far left and far right, in dark green, natural riparian ecotones can be detected along the rivers. (b–d) Source: NASA GeoCover circa 1990 Landsat images. False color composite of Landsat bands 7, 4, and 2. Green shades represent vegetation, magenta and brown represent bare soil, black represent water bodies, recent lava flows of shadows, cyan shades represent snow, and white represents clouds. Downloaded from Applied Sciences directorate (2006). From MDA Federal (2004). All images are public domain. Source for this dataset was the global Land Cover Facility, <http://www.landcover.org>. The figures were produced by Noam Levin.

the environment rapidly shifts from one type to another based on abiotic (e.g., climatic) and/or biotic (e.g., community structure) factors (Holland *et al.*, 1991; Kent *et al.*, 1997). The origin of the word “ecotone” is in the Greek roots “oikos” (home) and “tonus” (tension). Many different definitions and terms have been used in the literature to describe areas of ecological transition. These include boundary regions, borders, meeting zones, transitional zones, tension zones, zones of intermingling, and zones of transgression (Kent *et al.*, 1997). The definition often relates ecotones to more homogenous areas found on both sides of the transition or to the landscape as a whole. Ecotones can occur in both terrestrial and aquatic systems, and cover several spatial scales, from large spatial-scale ecotones, where biomes meet to local-scale transitions, such as mountain treelines (Gosz, 1993; see Fig. 1). These areas are sometimes considered to be dynamic zones of interaction between communities, which are unstable over time (Kent

et al., 1997). As suggested by Odum (1953), they do not simply represent a boundary or an edge; the concept of an ecotone assumes the existence of active interaction between two or more ecosystems with properties that do not exist in either of the adjacent ecosystems. Ecotonal regions show a diversity of boundary types that range from natural boundaries (e.g., altitudinal and latitudinal transitions) to human-generated ecotones, sometimes termed anthropogenic ecotones (e.g., forest clear-cut edges or urban ecotones) (Lloyd *et al.*, 2000), as shown in Fig. 1.

II. EARLY WORK ON THE EFFECTS OF ECOTONES ON BIODIVERSITY

Since the late nineteenth century, there has been interest in boundary regions and edges of ecological systems. A conceptual ecological framework for the

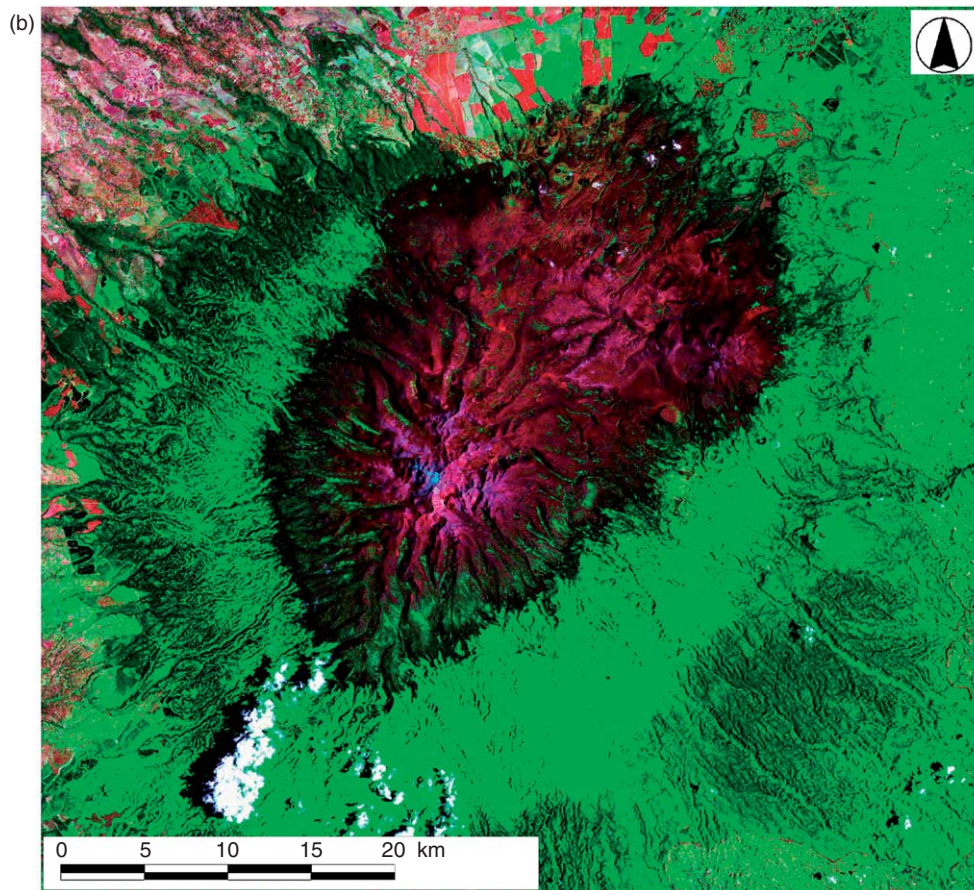


FIGURE 1 Continued

study of ecotones was given by Odum in 1953. He discussed the ecotone effect, which he characterized as increased richness and abundance in ecotones and the occurrence of unique ecotonal species. Until the 1970s, there was considerable interest in ecotones in the scientific community (reviewed by [Risser, 1995](#)). This interest subsided when a focus on more homogenous and well-defined ecosystems and communities (e.g., tropical rainforests and tundra) became common. A revival of research in the field focusing on ecotones and their effects on biodiversity was seen in the late 1980s and 1990s, with the development of new research areas, especially those of landscape ecology and of conservation biology ([Holland *et al.*, 1991](#)). Studies on ecotones in the 1980s often focused on material flow (e.g., water and nutrients) across communities and on ecosystem processes in these boundary regions ([Hansen and di Castri, 1992](#)). Much of the work focused on wetlands and on riparian zones, where land–water interfaces occur (reviewed in [Zalewski *et al.*, 2001](#)). Later work in the 1990s more

directly examined the effect of ecotones on biological diversity, and especially the relationship between ecotones and processes leading to morphological divergence, patterns of genetic and phenotypic diversity, species richness, rarity, and their conservation implications (reviewed in [Kark and van Rensburg, 2006](#)).

III. THE MEASUREMENT OF ECOTONES

Because ecotones can rarely be delimited by a fine line, their measurement and mapping is not trivial. A wide range of research approaches and tools have been used to detect and quantify ecotones. These include, among others, simulation modeling, geographic information systems (GIS), remote sensing, and statistical tools that enable quantification and analysis of ecotones of different types and over several spatial scales. Diverse approaches for the quantification of the steepness of gradients exist (reviewed in [Kark and van Rensburg, 2006](#)). Methods for measuring and characterizing

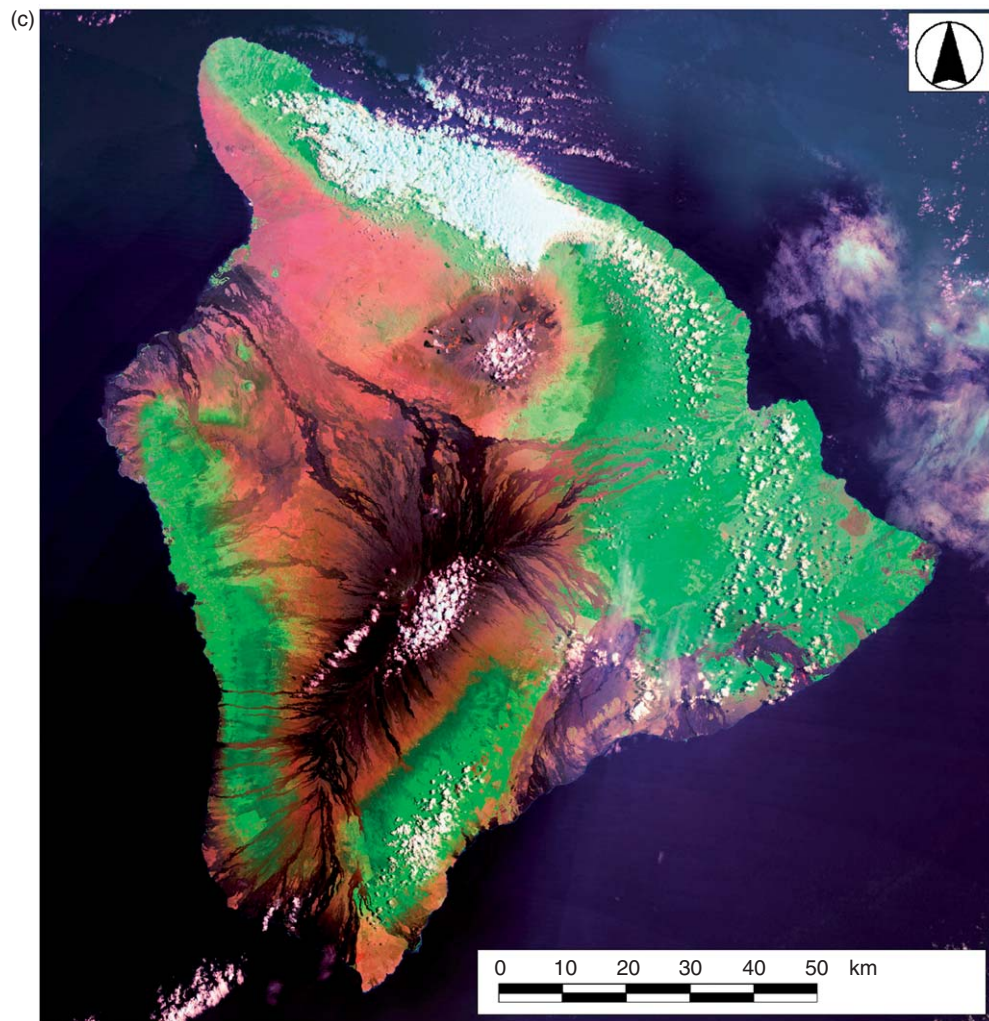


FIGURE 1 Continued

ecotones depend on the data available (e.g., quantitative or qualitative, grid- or transect-based data), with one of the simplest approaches, proposed by Womble in 1951, being the quantification of the magnitude of the first and second derivatives (rates of change in a given variable or several variables along a spatial gradient) (Womble, 1951). These approaches often examine the values of variables in an area (e.g., a 1×1 km grid square) relative to its neighboring regions. The basic idea is to detect areas of sharp transition (which are referred to as boundaries or ecotonal regions) by finding the areas with the highest rate of change in the value of a given variable or several variables between adjacent squares (pixels). Specific software for the analysis of boundary regions

are now available, enabling more widespread use of statistical tools for the study of ecotones (Fortin *et al.*, 2000).

In recent years, new approaches to quantify changes in diversity across gradients and boundary regions have been developed and applied. Among these is a range of new beta-diversity estimates of species turnover in space, which have been developed in the past decades since Wilson and Shmida's (1984) review on beta-diversity estimates. These are often used for studying gradients and do not focus on the ecotonal areas, yet can be applied for both purposes. One of the most promising directions in ecotone and boundary measurement is the use of tools developed in other areas of science. These include fields such as physics,

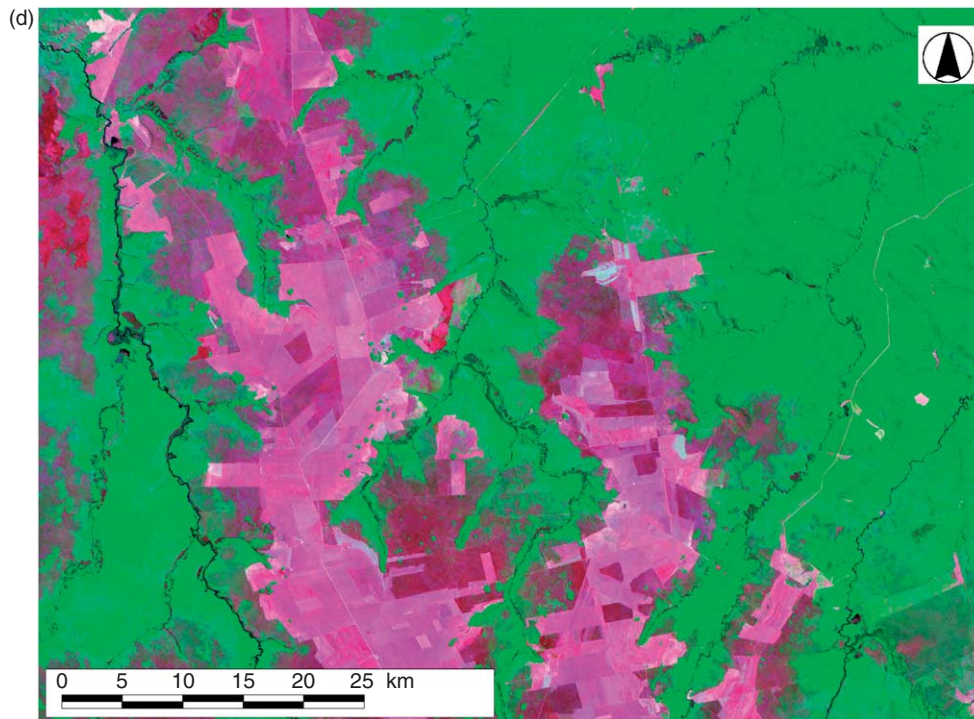


FIGURE 1 Continued

remote sensing, and image analysis, where substantial advancements in boundary detection and gradient quantification methods have been made. Remote-sensing tools, for example, can use data occurring over several orders of magnitude, from satellite-derived data currently available at a resolution of 0.5 m to 100 km, to electronic microscope data. Further application of these tools at multiple spatial resolutions will provide a better understanding of ecotones.

IV. PATTERNS OF BIODIVERSITY IN ECOTONES

Studies on patterns of biodiversity in ecotonal areas have led to a range of results. Recent work is providing increasing evidence that boundary regions between ecological communities can be highly diverse at both the within-species and community levels. Ecotones have been shown to hold especially high biological diversity over several spatial scales, at both the community level (when examining species richness, i.e., the number of species in an area, e.g., [Shmida and Wilson, 1985](#)) and at the within-species level (morphological and genetic diversity) as reviewed by [Kark](#)

[and van Rensburg \(2006\)](#). Other studies, however, have shown conflicting results, making it difficult to generalize without carefully examining each case, community, and region. Early on, [Odum \(1953\)](#) pointed at high species richness and abundance in ecotones and suggested that the ecotonal community commonly contains many species that are characteristic of, and sometimes restricted to, the ecotone. In a recent continental-scale study of New World birds, [Kark *et al.* \(2006\)](#) examined the relationship between passeriform richness and rarity of ~2300 passeriform species in 4889 one-degree New World grid cells and the distance of the cells to boundaries between adjacent plant-based ecoregions. They found that areas nearer to boundaries between ecoregions had more bird species, and also scored more highly in terms of species rarity. The findings of their work suggest that transitional environments harbor many rare species, in addition to high richness. At the community level, there is also some evidence for high species richness in ecotonal areas in marine systems. For example, in the Gulf of Aden, [Kemp and colleagues \(Kemp, 2000\)](#) found high-reef fish diversity in an ecotone harboring a unique mixing of the three distinct faunas of Oman, the Red Sea, and the Indian Ocean.

V. PROCESSES SHAPING BIODIVERSITY IN ECOTONES

A. Ecotones and Evolutionary Processes

The process by which new species form is called speciation. This process is of major interest to evolutionary biologists who define three major types of speciation: allopatric, parapatric, and sympatric. The three models are based on the degree of geographical subdivision between populations that lead to the formation of new species. Allopatric speciation happens in geographical isolation, and has been for many years considered the major form of speciation. Parapatric speciation occurs in adjacent populations with gene flow among them, often along clines. Sympatric speciation occurs when populations are geographically congruent, and are found in the same area. The study of ecotones has led to a better understanding of the potential importance of parapatric and sympatric speciation as mechanisms for speciation. Ecotones have been proposed to be centers of evolutionary novelty that maintain evolutionary process, and especially regions where parapatric (or sympatric) speciation processes may take place (Schilthuizen, 2000). As such, ecotones have been suggested as natural laboratories where evolutionary processes and barriers to gene flow can be examined (Schilthuizen, 2000). A review by Moritz *et al.* (2000) summarized the major models of evolutionary processes that promote diversification of rainforest faunas. They include the Gradient Model (either parapatric or sympatric), which suggests that adaptive divergence caused by selection forces occurs across sharp environmental gradients, leading to speciation even in the face of gene flow across ecotones. This means that speciation does not require isolation in cases where selection is strong enough to separate populations. This process is expected to occur especially where very different environments meet in the ecotone, for example, at the border between a dry and wet rainforest. In such regions, sharp boundaries may mean that even when gene flow continues, strong selection pressures can lead to divergence.

Support for the gradient model comes from recent research examining divergence using molecular genetic, phenotypic, and experimental approaches (Smith *et al.*, 1997; Schneider *et al.*, 1999; Moritz *et al.*, 2000; Schilthuizen, 2000). Smith *et al.* (1997), studying the little greenbul (*Andropadus virens*), a passeriform bird in the rainforest–savannah ecotone region of Cameroon, found especially high morphological divergence in the ecotone. They proposed that when the ecotone is large

enough, natural selection processes could be strong enough to generate morphological differences similar to those seen in reproductively isolated species even when high rates of gene flow occur. Their data support the divergence-with-gene-flow model of speciation (Smith *et al.*, 2000), leading them to propose that ecotones may be integral to the production and maintenance of high biodiversity in tropical rainforests. Increasing evidence suggests that ecotone regions may serve as centers for rainforest speciation. Quantification of morphological and geographic distances in olive sunbird (*Nectarinia olivacea*) populations in West African forests and ecotones revealed similar divergence patterns (Smith *et al.*, 2000). Smith studied morphological divergence in another Central African species, the black-bellied seedcracker (*Pyrenestes ostrinus*). Seedcrackers show polymorphism in bill size. A megabilled morph was found in the ecotone that specializes on a very hard-seeded sedge found only in ecotonal areas (Moritz *et al.*, 2000). This ecotonal megamorph was maintained in the population, despite high levels of gene flow with rainforest populations that had only smaller-billed morphs, owing to its selective advantage for feeding on the hard seeds. Morphological divergence between habitats across an ecotone was also found in leaf-litter skinks (*Carlia rubigularis*) in the wet tropical rainforest of Australia (Schneider *et al.*, 1999). Adult skinks occurring across sharp ecotones from open (wet sclerophyll) forests to adjacent rainforests showed large morphological and life history differences over short distances despite moderate to high levels of mitochondrial gene flow (Schneider *et al.*, 1999). Populations occurring across the ecotone had larger size differences than populations located dozens to hundreds of kilometers away that were geographically isolated millions of years ago, suggesting that in this case, and perhaps in many others that await research, speciation with gene flow may have great importance, even compared with allopatric speciation.

If boundary regions harbor 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 (neoenemics). Fjeldså and Rahbek (1998) suggested that more recently evolved species are concentrated in transitional ecotones surrounding the main central African rainforest. This reasoning is consistent with the finding that terrestrial ecotones sustain high morphological divergence, providing evidence that current speciation processes may indeed be taking

place in these regions (Moritz *et al.*, 2000; Schilthuizen, 2000; Smith *et al.*, 1997).

B. Ecotones, Gradients, Species Ranges, and Variability

What might lead to higher species richness in ecotonal regions compared with adjacent areas? Evolutionary processes, as discussed above, may be one explanation. Ecological factors may also have importance in shaping this pattern. Several authors, such as Gosz (1993) and Risser (1995) have suggested that transitional areas not only share the two types of environments of the habitats that coincide in the ecotone, but also have a unique ecotonal environment. Indeed, Odum (1953) proposed that transition zones often support a unique community with characteristics additional to those of the communities that adjoin the ecotone, although also commenting this is by no means a universal phenomenon. Studies testing these predictions show mixed results, some pointing toward the occurrence of ecotonal species, while others not finding evidence for species unique and highly abundant in ecotones. The inconsistency among studies is complicated by the fact that different species, systems, scales, and regions were used in different studies or due to methodological factors, such as differences in sampling and analysis approaches. In addition, ecotones tend to shift in space and time over several spatial scales (Gosz, 1993; Kent *et al.*, 1997), as a response to climatic variation and other environmental changes (Crumley, 1993; Neilson, 1993; Kent *et al.*, 1997). They show high spatial and temporal heterogeneity, which may serve as important factors contributing to their high genetic and species diversity (Risser, 1995). For example, multiple ecotones can be defined within and around the African Sahel (Fig. 1a), depending on the scale of interest and on the definitions used (Agnew and Chappell, 2000). The different transitions (e.g., that between the Sahel and the desert to the north) experience shifts in time and space, showing high spatiotemporal variability.

Another, simpler, process shaping this pattern is that ecotones, comprising meeting areas between adjoining communities, include a combination of species from two or more community types (Risser, 1995). Ecotonal areas often comprise the edge of the range for species on both sides and are where many peripheral populations occur (Shmida and Wilson, 1985; Kark and van Rensburg, 2006). An important question is whether populations occurring in ecotonal areas are viable populations that exist over time within ecotones, or are

rather present temporarily due to the constant flow of individuals from other parts of their range into the ecotone areas, and not self-sustainable over time, and will disappear if this flow is stopped. Shmida and Wilson (1985) proposed that the high number of species in transitional areas could be due to a process they called the mass effect, which is the flow of individuals from favorable to unfavorable areas. For species that reach the margins of their range at the ecotone, this effect may result in some individuals of a given species establishing in ecotonal areas where they cannot maintain viable populations, existing in sinks adjacent to larger source populations (Shmida and Wilson, 1985). This may lead to increased species richness in ecotonal areas, which is maintained by constant immigration of individuals from more favorable environments. 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 or genotypes. If some species or genotypes are characteristic of an ecotone or occur at the ecotone in higher abundances than in the neighboring habitats, as proposed above, this could suggest that some ecotone populations are ecologically viable. Several recent studies have found peak genetic and morphological diversity within species in ecotone regions, with populations in these regions harboring unique and rare alleles not found elsewhere (Kark and van Rensburg, 2006). For example, a study examining allozyme (protein level) diversity within chukar partridge (*Alectoris chukar*) populations across a rainfall gradient from northern to southern Israel found that the highest levels of diversity occurs in the sharp ecotone area between the Mediterranean region and the desert, in the northern Negev area. Populations in this area not only showed higher genetic diversity based on 32 loci (proteins) examined, but also had unique and rare alleles that did not occur elsewhere across the range. The same species also had peak levels of morphological diversity in the ecotone region based on 35 traits and 23 ratios between traits (reviewed in Kark and van Rensburg, 2006). More studies on genetic and species uniqueness in ecotonal areas are needed to enable generalizations.

1. Implications for Conservation

While an understanding of the effects of ecotones on biodiversity is important for evolutionary and

ecological pure science purposes, it also has many implications for conservation of biodiversity and practical decision making. Some scientists have argued that because ecotones hold marginal populations at the edge of the range of many species, where abundances may be lower and populations more prone to local extinctions, than other parts of the range, these ecotonal areas have low value for conservation as they will not persist over time, for example, if the surrounding environments become fragmented (e.g., [Gaston *et al.*, 2001](#)). There has been an interesting discussion in the literature in recent years regarding whether transitional areas are valuable for conservation (e.g., see [Smith *et al.*, 2001](#) versus [Brooks, 2001](#)). Substantial conservation attention has been given in recent years to the understanding and mapping of biodiversity patterns and the underlying processes, and toward predicting the effects of global change. 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 ([Crumley, 1993](#); [Neilson, 1993](#); [Allen and Breshears, 1998](#)). In addition, while some scientists suggest that ecotone populations are more likely to be negatively affected by climate change ([Gaston *et al.*, 2001](#)), other researchers have argued that ecotonal areas sustain populations that are adapted to changing, fluctuating, and unstable environments and, as such, these populations may be better able to persist in the face of predicted change (see further discussion in [Kark and van Rensburg, 2006](#)). This is especially relevant since climate shifts are expected, according to some studies, to be rapid and extreme in boundary regions between ecosystems ([Allen and Breshears, 1998](#)). By examining changes in ecotone locations over time, these areas may potentially serve as “early warning” indicators of global changes ([Crumley, 1993](#); [Neilson, 1993](#)). However, the response depends on the spatial and temporal scales examined and may be a useful indicator mainly at global spatial scales and rather coarse timescales. Therefore, this area deserves further attention owing to the complexity of the factors affecting the location of ecotones in space and time.

Much research in recent years has focused on prioritizing conservation efforts and determining what areas are most important and valuable for conservation. Two main approaches have been suggested. The first approach includes a search for biodiversity hotspots, or areas with especially high species richness, endemism, and rarity. A second approach has been to select areas

that are complementary, and hold biodiversity not present in other areas. Ecotones may provide a unique opportunity to conserve both high species richness and high complementarity, although this idea is still being debated. Undoubtedly, if these areas have the potential to maintain and to generate species richness as well as unique and novel species and forms, they deserve far greater research attention than they are currently receiving ([Smith *et al.*, 2001](#)). Nevertheless, conservation plans for ecotones should not be considered independent of their surrounding environments. Ecotonal regions are important for our understanding of evolutionary (such as speciation, divergence with gene flow, and adaptation) and ecological processes shaping biodiversity (e.g., response of populations to fluctuating environments). They may enable us to predict the responses of populations to environmental change better and to further identify previously neglected biodiversity hotspots valuable for biodiversity research and conservation.

C. Human-Related Ecotones

While early ecotone literature largely dealt with natural ecotones that are generated by environmental factors such as soils, geology, and sharp climatic gradients, recent research is increasingly including human-related boundaries. Human activity is generating boundaries that did not exist before, changing their steepness and shifting their location. These boundaries include a diversity of ecotone types, such as forest clear-cut edges, margins between built-up and natural landscapes, and human-generated features, such as lakes and plantations. Research on these human-generated ecotones and their effects on biodiversity is related to a study area that is sometimes termed “countryside biogeography,” examining biodiversity in human-dominated landscapes. Another recently developing research area that is relevant is that of urban ecology. Sharp, human-caused transitions may result from human activities such as urbanization, land-use changes, agriculture, grazing, or burning (see [Fig. 1](#)). These boundaries occur at multiple spatial scales, ranging from local ecotones between agricultural plots, urban areas, and roads, and their neighboring native habitat, to large-scale ecotones such as shifting desert borders owing to desertification processes and river divergence ([Fig. 1](#)). These ecotones may be either static and fixed in space or dynamic and shifting in location over space and time.

A substantial amount of work in both natural and human-related landscapes has focused on what has been called the “edge effect.” This is the effect of the

juxtaposition of contrasting environments on an ecosystem. It refers to how the local environment changes along some type of boundary, or edge and how biodiversity is affected by such edges. This idea is attributed by animal ecologists to Aldo Leopold and his 1933 book *Game Management*. It encompasses a wide range of both biotic and abiotic trends associated with boundaries between adjacent habitat types, natural or anthropogenic. Much of the reference to edge effects in the recent landscape ecology literature has been related to human-caused boundaries, and especially to boundaries between forest fragments and neighboring patches of habitat that have been cleared. Again, there are no clear-cut conclusions as to the effect of human-dominated boundaries on biodiversity. The response largely depends on the type of edge and its history as well the species in focus. Its conservation implications are therefore complex and deserve further scientific attention. A vast amount of research has been done on the effect of forest edges, especially the effect of human-made fragments and their edges on biodiversity. A review of edges (Murcia, 1995) suggested there are many discrepancies in the literature, and a better understanding and search for general patterns requires a much more mechanistic approach to examine the processes underlying such patterns. In this context, there has been much effort to understand the effect of forest edges on predation, brood parasitism, and the breeding success of birds. Paton (1994) found that in the majority of studies, nest success varied near edges with an increase in both depredation and brood parasitism rates. The most conclusive studies suggest that edge effects in birds usually occur within 50 m of an edge (Paton, 1994). Since these reviews, multiple studies on dozens of species and regions have been conducted. While results show mixed patterns, small and intermediate-sized fragments of natural habitat (e.g., forest) tend to show stronger edge effects than large fragments.

VI. CONCLUSIONS

Research on the effect of ecotones on biodiversity suggests that these areas of sharp transition are, at least in some cases, centers of high species richness, genetic and phenotypic diversity, and that they can hold unique forms or species that are less abundant or do not occur elsewhere. In addition, studies suggest that ecotones are areas where populations are diverging to new species in the face of gene flow (across the ecotone). However, these patterns are not repeated in all

systems and we cannot yet say how general they are. Thus, the importance of ecotones to the generation and conservation of biodiversity, especially in the face of global climate and other changes, is an area of active research interest.

Acknowledgments

My thanks to Noam Levin for his help in generating the figure. This work was supported by the Israel Science Foundation (grant no. 740/04 to SK).

See Also the Following Articles

BIODIVERSITY, DEFINITION OF • HERBACEOUS VEGETATION, SPECIES RICHNESS IN • REMOTE SENSING AND IMAGE PROCESSING

Bibliography

- Agnew, C. T., and Chappell, A. (2000). Drought in the Sahel. *Geol. J.* 48, 299–311.
- Allen, C. D., and Breshears, D. D. (1998). Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *Proc. Natl. Acad. Sci.* 95, 14839–14842.
- Applied Sciences directorate, <https://zulu.ssc.nasa.gov/mrsid/> (accessed November 2006).
- Brooks, T. M. (2001). Prioritizing hotspots, representing transitions. *Trends Ecol. Evol.* 16, 673.
- Crumley, C. L. (1993). Analyzing historic ecotonal shifts. *Ecol. Appl.* 3, 377–384.
- Fjeldså, J., and Rahbek, C. (1998). Continent-wide conservation priorities and diversification processes. In *Conservation in a Changing World* (G. Mace, A. Balmford, and J. Ginsberg, Eds.), pp. 107–138. Cambridge University Press, Cambridge.
- Fortin, M.-J., Olson, R. J., Ferson, S., et al. (2000). Issues related to the detection of boundaries. *Landscape Ecol.* 15, 453–466.
- Gaston, K. J., Rodrigues, A. S. L., van Rensburg, B. J., Koleff, P., and Chown, S. L. (2001). Complementary representation and zones of ecological transition. *Ecol. Lett.* 4, 4–9.
- Gosz, J. R. (1993). Ecotone hierarchies. *Ecol. Appl.* 3, 369–376.
- Hansen, A., and Di Castri, F. (1992). *Landscape Boundaries: Consequences for Biotic Diversity and Ecological Flows*. Springer, New York.
- Holland, M., Risser, P., and Naiman, R. (1991). *Ecotones*. Chapman & Hall, New York.
- Kark, S., Allnutt, T. F., Levin, N., Manne, L. L., and Williams, P. H. (2006). The role of transitional areas as avian biodiversity centres. *Global Ecol. Biogeogr.*, doi: 10.1111/j.1466-8238.2006.00274.X
- Kark, S., and van Rensburg, B. J. (2006). Ecotones: Marginal or central areas of transition? *Israel J. Ecol. Evol.* 52, 29–53.
- Kemp, J. M. (2000). Zoogeography of the coral reef fishes of the north-eastern Gulf of Aden, with eight new records of reef fishes from Arabia. *Fauna Arabia* 18, 293–321.
- Kent, M., Gill, W. J., Weaver, R. E., and Armitage, R. P. (1997). Landscape and plant community boundaries in biogeography. *Prog. Phys. Geogr.* 21, 315–353.

- Kunin, W. E. (1998). Biodiversity at the edge: A test of the importance of spatial "mass effects" in the Rothamsted Park Grass experiments. *Proc. Natl. Acad. Sci.* **95**, 207–212.
- Lloyd, K. M., McQueen, A. A. M., Lee, B. J., Wilson, R. C. B., Walker, S., and Wilson, J. B. (2000). Evidence on ecotone concepts from switch, environmental and anthropogenic ecotones. *J. Veg. Sci.* **11**, 903–910.
- MDA Federal (2004) Landsat Geocover (1990/TM) Edition Mosaics; Tiles N-37-00 and S-37-00 (Mt. Kenya), N-14-15.20 (Hawaii), and S-21-10 (Amazon). US Geological Survey, Sioux Falls, South Dakota.
- Moritz, C., Patton, J. L., Schneider, C. J., and Smith, A. R. (2000). Diversification of rainforest faunas: An integrated molecular approach. *Annu. Rev. Ecol. Syst.* **31**, 533–563.
- Murcia, C. (1995). Edge effects in fragmented forests: Implications for conservation. *Trends Ecol. Evol.* **10**, 58–62.
- Neilson, R. P. (1993). Transient ecotone response to climate change: Some conceptual and modelling approaches. *Ecol. Appl.* **3**, 385–395.
- Odum, E. P. (1953). *Fundamentals of Ecology*. W. B. Saunders Company, Philadelphia.
- Paton, P. W. C. (1994). The effect of edge on avian nest success: How strong is the evidence? *Conserv. Biol.* **8**, 17–26.
- Risser, P. G. (1995). The status of the science examining ecotones. *BioScience* **45**, 318–325.
- Schilthuizen, M. (2000). Ecotone: Speciation-prone. *Trends Ecol. Evol.* **15**, 130–131.
- Schneider, C. J., Smith, T. B., Larison, B., and Moritz, C. (1999). A test of alternative models of diversification in tropical rainforests: Ecological gradients vs. rainforest refugia. *Proc. Natl. Acad. Sci.* **96**, 13869–13873.
- Shmida, A., and Wilson, M. V. (1985). Biological determinants of species diversity. *J. Biogeogr.* **12**, 1–20.
- Smith, T. B., Kark, S., Schneider, C. J., Wayne, R. K., and Moritz, C. (2001). Biodiversity hotspots and beyond: The need for conserving environmental transitions. *Trends Ecol. Evol.* **16**, 431.
- Smith, T. B., Wayne, R. K., Girman, D. J., and Bruford, M. W. (1997). A role for ecotones in generating rainforest biodiversity. *Science* **276**, 1855–1857.
- Smith, T. B., Wayne, R. K., Girman, D. J., and Bruford, M. W. (2000). Evaluating the divergence-with-gene-flow model in natural populations: The importance of ecotones in rainforest speciation. In *Rainforests Past and Future* (E. Bermingham, C. W. Dick, and C. Moritz, Eds.), pp. 148–165. University of Chicago Press, Chicago.
- Stöckli, R., Vermote, E., Saleous, N., Simmon, R., and Herring, D. (2005). *The Blue Marble Next Generation—A True Color Earth Dataset Including Seasonal Dynamics from MODIS*. NASA Earth Observatory, Goddard Space Flight Center, Greenbelt, MD, USA.
- van Rensburg, B. J., Koleff, P., Gaston, K. J., and Chown, S. L. (2004). Spatial congruence of ecological transition at the regional scale in South Africa. *J. Biogeogr.* **31**, 843–854.
- Visible Earth, <http://visibleearth.nasa.gov/> (accessed November 2006).
- Wilson, M. V., and Shmida, A. (1984). Measuring beta diversity with presence-absence data. *J. Ecol.* **72**, 1055–1064.
- Womble, W. H. (1951). Differential systematics. *Science* **114**, 315–322.
- Zalewski, M., Schiemer, F., and Thorpe, J. (2001). Fish and land-inland water ecotones: Overview and synthesis. *Ecohydrol. Hydrobiol.* **1**, 261–266.