ECOTONE HIERARCHIES

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Abstract. Ecological phenomena are evident over a broad spectrum of space and time scales. Ecotones, being defined as zones of transition between adjacent ecological systems, also must occur over an equally broad spectrum of space and time scales. Scale-dependent constraints influence ecological phenomena and resulting zones of transition; however, in traditional ecotone studies little treatment has been given to these influences. This paper addresses aspects of the ecotone concept that relate to the strength of interactions between adjacent systems for a hierarchy of ecotones in a biome transition area in central New Mexico on the Sevilleta National Wildlife Refuge. Zones of transition occur at plant, population, patch, landscape, and biome levels in the hierarchy suggested here. Constraints differ across this hierarchy, primarily because of the different scales at which these constraints exert their influences. The basic strategy to understand these cross-scale influences must be to perform studies at different scales, and a hierarchical approach identifies those scales. This also is important for identifying the appropriate technologies that focus at the scales where transition zones between ecological systems/phenomena are expressed. A broad array of technologies are available for integrating the pattern–process relationships that occur across the many scales in ecological systems.

Key words: biome; dynamics; ecotone; hierarchy; interactions; remote imaging; Sevilleta, New Mexico; threshold; transition.

INTRODUCTION

Ecotone: a zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems (Holland 1988). This definition proposed by a working group in Paris in 1987 was recognized as being general; however, it also was agreed that it was a necessary launching point for development of the theoretical base necessary for future discussions of the ecotone concept.

Ecotonal phenomena are evident over a broad spectrum of space and time scales, and studies need to adopt a multi-scale perspective performing studies at several scales (Gosz 1991). An important focus must be on linkages between domains of scale, as called for by Meentemeyer and Box (1987): a "science of scale." Often a hierarchy of scales is proposed; however, such arrangements do not mean that we understand how to translate the pattern–process relationships associated with ecotones across the nonlinear spaces between domains of scale (Gosz 1991). We are only likely to recognize such linkages when we identify how different hierarchical levels constrain one another (Weins 1989) as well as the different types of contraints that dominate at particular scales. These scale-dependent constraints are related to different strengths of interactions between adjacent systems.

This paper will address aspects of the ecotone concept that relate to the strength of the interactions between adjacent systems, for a hierarchy of ecotones in a biome transition area. The example in this paper identifies studies of ecotones at different space and time scales that are used to translate pattern–process relationships for this biome transition zone.

THE ECOTONE HIERARCHY

Table 1 depicts a hierarchy of ecotones ranging from the biome ecotone (i.e., biome transition area) to the plant ecotone. The traditional types of ecotones included are those of the patch (Forman and Godron 1986) and biome (Gosz and Sharpe 1989, Gosz 1991, Neilson 1991). The hierarchy in Table 1 adds additional levels, down to the transition that occurs at a

![Fig. 1. Hypothetical biome transition zone reflecting the mosaic pattern across the zone separating the two biomes (biome ecotone). The pattern changes from relatively large patches in the core area of each biome to small patches at the ecotone. Environmental changes that result in biome movement should cause a displacement of the mosaic pattern.](image-url)
FIG. 2. Ecotone diagram and occurrence of three species in the ecotone. (A) Schematic representation of the extent of range of the three study species along a 10-km transect in the Sevilleta, New Mexico, biome transition area, and the location of the three study sites. The arrows indicate relative direction and degree of movement for the three dominant species in this biome ecotone. (B), (C), and (D) Patch size and abundance of Larrea tridentata, Bouteloua eriophora, and B. gracilis. Note the scale changes in these patch-size graphs. Larrea was not encountered at the northern end of the transect (Deep Well study plot), and B. gracilis was not encountered at the southern end of the transect (La Joya study plot).

The reason for these additional levels is to increase the number of scales of study and the ability to extrapolate between them. For example, the landscape ecotone relates to a transition in the mosaic pattern that is characteristic of an ecotone between two biomes. The mosaic pattern is made up of variations in the number and sizes of patches that represent the two biome types (Fig. 1). There are many patch ecotones in a biome ecotone, and it is likely that there is a spectrum of patch-interaction processes depending on the juxtaposition, size, substrate patterns, and distances between patch types. A study of one patch ecotone cannot completely characterize or be extrapolated to the biome ecotone.

At the other end of the hierarchy is the plant-edge ecotone. Measurements at the 1-m² scale often characterize plant edges. At this scale the two ecological systems are the different microclimates, soil chemistries, and soil fauna and flora that occur under a plant canopy vs. in the open or under a different plant canopy. The level between the patch and the plant ecotone is identified as a population ecotone. This represents the spatial pattern of the population of individual plants of a certain species and is similar conceptually to the
spatial pattern (mosaic) of patches in the landscape ecotone. Where landscape patches are dominated by one plant species, the population and patch levels are identical. We expect a spectrum of individual plant-edge interactions for the mosaic representing the population that depends on the juxtaposition, sizes of plants, distance between neighbors, understory species, and plant species interactions. No single plant-edge study (i.e., 1-m² plot) can characterize the population or patch. The strengths of the interactions between populations are influenced by population sizes, spatial arrangements, distances from other subpopulations, etc., and are well documented in the literature. The challenge is to develop procedures to interrelate processes and constraints at these different levels to allow interpretations at all levels.

**ECOTONE CONSTRAINTS**

Table 1 also suggests probable constraints that can be dominant on the different ecotone hierarchies. It seems clear that at the biome scale, climate (expressed through weather) interacting with macrotopography constrains the species of a particular life-form that characterizes a biome (Neilson 1991). In contrast, at the scale of individual plant edges, climate and macrotopography are constants, and the controls are likely to be factors such as microclimatology, microsite factors (soil moisture, chemistry), plant genetics expressed through plant chemistry, physiology, competition, and plant–animal interactions. The constraints at intermediate scales are characterized by a progression of overlapping controls that operate at those intermediate
scales. The point is that different constraints operate at different levels, and studies extrapolating across scales need to integrate across the different constraints as well.

Another point made in Table 1 is that, in addition to different controls dominating the finer scales (e.g., plant ecotone), there is an increase in the number of probable controls and interactions between them at these finer scales. This contributes to the increased variation at fine scales as well as the difficulty in modelling and predicting responses. The spectrum of results for interactions at fine scales is potentially larger and more variable than the spectrum at broad scales. Much of the fine-scale variation is integrated (or averaged out) at broad scales, leaving only the broad-scale constraints correlated with broad-scale ecotone patterns that change over broad (long) temporal scales.

**Threshold Behavior**

Gosz (1991) suggested that spatial patterns in landscapes have nonnormal, spatially autocorrelated, non-stationary, discontinuous, and irregularly spaced parameters. The dynamics of ecotones in landscapes also are likely to be nonlinear, perhaps chaotic, and can behave in ways that are not simple averages of adjacent resource patches (Naiman et al. 1988, Gosz and Sharpe 1989). Threshold dynamics are expected to occur near boundaries. Biological systems are metastable (O'Neill et al. 1989), meaning that the properties of the landscape remain stable only over a limited range of conditions. As those conditions reach a critical threshold, the system may reach a discontinuity (i.e., bifurcation) resulting in a radical change in the system state. O'Neill et al. (1989) discussed potential methods for detecting the instability near such bifurcation points: (1) increases in the relaxation time from small perturbations could be measured directly; and (2) increases in the variance of observed fluctuations before the discontinuity.

The spatial patterns of ecotones provide a spatial analog for these temporal dynamics. A transect across an ecotone is expected to show increased spatial variation (e.g., increased numbers of small patches of different species) at the ecotone (see next section). Temporal studies are expected to show the greatest variation in spatial change at the ecotone as microsites change from one community to another. Away from the ecotone the changes are primarily an increase in the diameter of the patch rather than a state change. The exception to this might be the change of an entire biome (e.g., forest to savanna) if the climate changes. This would be an ecotone in time (Neilson 1991).

Grover and Musick (1990) describe a ratchet–pulse dynamic for landscape change in a transitional area. Certain microsites or landscape facets are at a threshold with respect to the conditions allowing the persistence of a certain community. Relatively small changes that exceed the threshold conditions (e.g., three successive dry years) cause certain sites to be changed to a different community while the others remain unchanged. In these areas the pattern of wet vs. dry, cold vs. hot years may be more influential than the conditions of any single year. The effectiveness of a pattern of wet or dry years in causing change may also be related to the life-history strategies of the plant species. Most plant species have strategies (e.g., long-lived, seed banks) that allow tolerance of short periods of stress relative to the life-history strategy. Certain microsites or landscape facets magnify the influence of a climatic signal or reduce the effectiveness of the life-history strategy for some species, resulting in mortality and/or new establishment.

The temporal and spatial dynamics of ecotone communities are alleged to be much more variable than those of biome or patch core areas. This variability may be seen as a curse or a benefit. For research programs that utilize variability as a sensitive indicator of environmental change, ecotones are logical areas for study.

**Sevilleta National Wildlife Refuge Case Study**

The Sevilleta National Wildlife Refuge (NWR) is a Long-Term Ecological Research (LTER) site in New Mexico. This site is in a biome transition area where these multi-scale studies are being performed to develop cross-scale extrapolations and explanations. Figs. 2–5 demonstrate some of the intermediate-scale results that are being used to relate plant to biome extrapolations. In a biome transition zone, species respond in an individualistic manner to the gradients of factors limiting their ranges. Fig. 2 demonstrates that dominant species of two biomes—Great Plains Short-Grass Steppe and Chihuahuan Desert—have been able to in-
FIG. 3. Aerial photograph (scale = 1:10 000) showing mosaics of the dominant species in the Sevilleta biome transition area. In this image, the darker patches are dominated by *Bouteloua gracilis* on Haplargid soils and the lighter patches are *B. eripoda* on Calciorthid soils. The small dot features identify kangaroo rat (*Dipodomys spectabilis*) mounds.

The results shown in Fig. 2 represent a snapshot in time of the changing patterns. A comparison of site photographs from 1915 and 1990 demonstrates marked movement of *L. tridentata* in the ecotonal area of the transect and a movement of the mosaic pattern hypothesized in Fig. 1 (J. Betancourt, unpublished photographs). Aircraft photography is a valuable technology for evaluating the ecotonal dynamics of broader-scale features (Fig. 3). Studies of a series of air photos (1935–1984) have identified directional movement of populations of these life-forms and mosaic patterns (*B. Musick, unpublished data*). Long-term measurements of the line-intercept transects in the 1-km² study areas (Fig. 2) will quantify the dynamics of this broad-scale mosaic pattern. The photos also detect broader-scale patterns of other species (*e.g.*, *B. eripoda*, *B. gracilis*) controlled by soil substrates. In Fig. 3, the dark-colored patches are dominated by *B. gracilis* on Haplargid soils and the light-colored patches are *B. eripoda* on Calciorthid soils. The small dots identify kangaroo rat (*Dipodomys spectabilis*) mounds. This rodent may be an important vector in the movement of plant species across the ecotone, through disturbance and dispersal activities.

The mechanistic explanations for the dynamics of the mosaic patterns come from studies of lower level ecotones. Finer scale studies along the transect on the Sevilleta NWR demonstrate the dynamics of plant edges. Figs. 4 and 5 show patterns of movement for individual plants during dry (1990) and wet (1991) summer conditions. The figures are computer-analyzed photographs of 3 × 4 m plots taken with a boom-mounted camera. The plots were photographed in the spring and autumn. The photographs were digitized and classified into plant and bare ground areas, and the images were overlaid to identify changes for the interval. This technology provides a nondestructive analysis of the same plot through time. Traditional methods of vegetation analysis tend to be slow because they are labor intensive and involve destructive sampling (*e.g.*, clipping). As a result, they are often confined to relatively few and small, local area measurements, and rely on statistical techniques to quantify change rather than repeat analyses of the same vegetation. With image-processing techniques such as that used for Figs. 4 and 5, numerous plots (*i.e.*, many hundreds) can be analyzed throughout the transition area to quantify the fine-scale changes associated with broad-scale changes in patch pattern. The image-processing soft-

vade (or be eliminated) to different degrees along a transect in the Sevilleta LTER study area. The species arrows indicate relative directions and extent of movement of these three species along the transect. The graphs show the abundance and sizes of patches of these dominants. The graph results are based on 1600 m of transect lines (1-cm resolution) in each of three, 1-km² study areas—Deep Well, Five Points, and La Joya—along the 10-km gradient. The patterns of these three species support the concepts of the individualistic nature of movement and the change in patch scale as the distribution limit is reached. In this case the patches also are population mosaics since the patch was identified by the occurrence of a single dominant species. Each species demonstrates a decreasing patch size as it approaches the limits of its distribution along the transect. *Bouteloua eripoda* and *Larrea tridentata* are Chihuahuan species; however, *B. eripoda* has extended further north than *L. tridentata*. *Bouteloua gracilis* is a Great Plains species and its patch size decreases to the south. The decreased patch size in these ecotonal areas is hypothesized to be a response to increased sensitivity to microsite conditions at the range limits of a species. It also reflects the individualistic nature of species movement; *i.e.*, germination and establishment patterns, which are influenced by the interaction of environmental conditions with the microsite environments. The net result of the patch patterns for these species is increased patch heterogeneity and a fine-grained mosaic pattern in the ecotone (Neilson 1991; Fig. 1). The transect represented in Fig. 2 is one of many patch ecotones in the biome mosaic. The pattern is expected to be common across virtually all ecotones in the region.

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ware used in these studies is Khoros—a robust system that makes it possible to perform the classification process by supplying the necessary tools to construct new algorithms and by supplying visualization and graphical user-interface tools (Rasure et al. 1990). The system has been developed into a turn-key production technology to allow rapid digitization and classification of the many photos being collected on the Sevilleta.

The plots in Figs. 4 and 5 have mixtures of *B. eripoda* and *B. gracilis*. Fig. 4 shows that there was virtually no change in plant cover of either species for the dry summer of 1990. The plant cover was 67% in both June and October and the small amount of area that changed from bare ground to vegetation (13%) was balanced by mortality/senescence causing conversion of plant cover to bare ground. During the wet summer of 1991 (Fig. 5), *B. eripoda* was very dynamic and almost entirely responsible for the plant cover increase from 49 to 80%. This was caused by expansion of individual plants into former bare-ground areas. *B. eripoda* (Chihuahuan species) is expected to respond primarily to summer precipitation (i.e., shallow root system) while *B. gracilis* (Great Plains Steppe) may gain a competitive edge from the deeper soil moisture that occurs following wet winter/spring conditions. *B. eripoda* is able to expand rapidly during years with wet summers through vegetative tillering, the mechanistic cause of patch area changes demonstrated in the transect studies. The high seed production during these years also may allow the establishment of additional plants, the initiation of new patches in the mosaic, and an extension of its range. Neilson (1986) reported that only 7 yr during the period 1915 to 1968 had significant seed production and establishment of *B. eripoda* on the Jornada site (Chihuahuan Desert) in southern New Mexico. These years occurred during periods of winter drought, sandwiched between periods of winter wet, but only when the dry winter was followed by high summer rainfall. Unique combinations of conditions also may allow *L. tridentata* to increase its patch size and extension to the north. A trend of dry summers combined with wet springs could cause *B. gracilis* to change its mosaic structure and a movement of the mosaic pattern to the south. These results identify the importance of temporal patterns or periodicities (i.e., temporal scales) in extremes of temperature and precipitation in this region and the important link with ecotone dynamics. The long-term studies possible with this LTER site will allow identification of the conditions and constraints controlling species in this transition zone.

**Cross-scale extrapolation and evaluation**

The combination of studies at different scales and over time, illustrated above, allows the extrapolation between scales needed for an understanding of the controls on the dynamics of the mosaic of the transition zone. Fig. 6 represents the multi-level, nested sampling design that relates plant-edge ecotones to the dynamics of the biome ecotone. Remotely sensed imagery is the likely technology to evaluate biome dynamics of the entire area, and the new technologies that evaluate images at the plant ecotone, population ecotone, and patch ecotone allow the basic integration across those scales. These studies can be coupled with traditional plot-clipping and line-intercept studies to reduce the otherwise intense field methodology to a minimum without a loss of information. The study transects and plots are expected to be diagnostic of dynamics that occur on the multiple ecotones in the area. Future studies on
additional ecotones will be used to validate the extrapolations of current results.

New capabilities in supercomputing and networking also will make cross-scale extrapolation feasible. For example, current plans are to obtain color aerial photography at a scale of 1:7920 (1 cm = 79.2 m). Each photograph would cover $\approx 3.28$ km$^2$ with the resolution of the color film (Film Code 2448) allowing the distinguishing of an object on the ground that is 18 cm in diameter (R. Parmenter, personal communication). The photos will have 70% overlap along the flight path to allow stereo imagery. It is estimated that 1000 of these photos would be needed to cover the 1300-km$^2$ area of the refuge and borderline areas. These photos could then be used to create digitized orthographic photos that would be incorporated into the Sevilleta Geographic Information System (GIS). Decision-based rules can be used to subsample the entire area to create images at different scales. For example, subsampling often results in the loss of information on spatial pattern in the original data. It is similar to averaging out variation. A rule that subsamples but maintains the fractal dimension of the fine-scale pattern produces a broad-scale pattern without losing structural information (B. Milne, personal communication). Scale-dependent analyses of the orthographic data set then provide standards for analyses that compare different technologies (satellite vs. aircraft vs. ground-based transects). The analyses also allow corrections for problems with results that are dependent on the technique used (i.e., different techniques utilize different assumptions that influence interpretations). The multiple data sets allow calibrated/referenced image-GIS analyses that provide needed information on vegetation-
soil relationships, plant distribution patterns, and the extent and pattern of animal disturbances in the ecotone hierarchy of this biome transition area.

In view of the enormous data storage, image-processing software requirements, and computing requirements to process data from the entire array of 1000 images, it will be necessary to develop interactive computing with supercomputer facilities. Each color photo requires 232 megabytes (MB) of storage (77.4 MB in each of red, green, and blue bands) and the 1000 photos necessary for the entire area require 232 320 MB (G. Shore, personal communication). We intend to utilize the national network to initiate processing requests from the Sevilleta computers, have processing performed on a supercomputer (e.g., San Diego [California] SuperComputing Center) with data in storage there, and output the results back to the Sevilleta computers. This approach will dramatically increase our ability to perform the scale-dependent analyses and cross-scale extrapolations called for in our hypotheses of biome transition dynamics.

**CONCLUSIONS**

This discussion of ecotone hierarchies emphasizes the scale-dependent nature of patterns and processes associated with ecotones. An edge at one scale may be indistinguishable at a different scale. However, the processes that occur at a certain scale can have significant influences on both broader and finer scales. Measuring and understanding these cross-scale influences represents a significant challenge for ecotone studies. The basic strategy must be studies performed at a number of scales, and this paper suggests one hierarchical classification to identify appropriate scales (i.e., plant edge to biome edge). Different technologies and approaches must be used at these different scales, requiring additional studies on integration and calibration of the techniques. A gradient analysis in a biome transition zone is one example where the different technologies are performed on the same transects to allow such cross-calibration. This analysis also allows the identification of the fine-scale properties that determine changes in properties in the next broader scale. The high variance associated with fine-scale measurements requires large sample sizes; however, some techniques, such as repeat photography on areas stratified by factors that act as constraints (e.g., topography, soil characteristics), can detect change with a minimal sample size.

The availability of supercomputing technologies allows additional capabilities for cross-scale integration. Complete area photography at fine resolution is possible, and the storage and computing capabilities at these supercomputing centers allows analyses of these huge data sets. The same digitized data base can be analyzed at fine to broad scales by a variety of decision-based rules that retain the properties of the different scales (e.g., fractals). These analyses also are able to identify the emergent properties that occur as scales are changed. Finally, such data bases act as the standard to allow comparisons of other techniques (e.g., satellite imagery, line-intercept transects, etc.). Such a multiscale, multi-technology approach will be a necessity for the challenge we have set for modelling ecotone dynamics.

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**LITERATURE CITED**


