Perspective

Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales

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Abstract

Human modification of landscapes overlying natural environmental heterogeneity is resulting in an increase in the numbers and types of ecological patches and their intervening boundaries. In this paper, we describe an operational framework for understanding and predicting dynamics of these biotic transitions for a range of environmental conditions across multiple spatial scales. We define biotic transitions as the boundary and the neighboring states, a more general definition than typically denoted by the terms boundary, ecotone, edge or gradient. We use concepts of patch dynamics to understand the structural properties of biotic transitions and to predict changes in boundaries through time and across space. We develop testable hypotheses, and illustrate the utility of our approach with examples from arid and semiarid ecosystems. Our framework provides new insights and predictions as to how landscapes may respond to future changes in climate and other environmental drivers.

Introduction

The structure of landscapes is complex and rarely homogeneous. Human modifications have greatly increased fragmentation such that landscapes are increasingly populated by a mosaic of distinct patches and intervening boundaries (ecotones) as well as more gradual changes in biota, all of which may respond differently to environmental drivers (Noss and Csuti 1997). Although a number of studies have been conducted on boundary structure at multiple spatial scales (e.g., Curtis 1959; Wiens et al. 1985; Cadenasso et al. 2003; Walker

et al. 2003), we have very little understanding of, and hence a low ability to predict, boundary dynamics: how boundaries form, how they change through time, and the processes and feedback mechanisms that govern changes in the location and composition of boundaries through time. However, boundary dynamics are key drivers of landscape change. We hypothesize that integrating concepts of patch and boundary dynamics has the potential to improve our understanding of and predictions about boundary processes and landscape dynamics. A clearer understanding of the relationship between patches and boundaries is

needed to predict how landscapes will respond to future changes in environmental drivers, such as climate and landuse (Kareiva and Wennergren 1995).

In general, the concepts of boundaries, ecotones, and patch dynamics have developed independently. Boundaries or edges are often viewed as barriers, constraints, or limits to the movement of animals and plants (e.g., Fagan et al. 1999; Lidicker 1999) whereas ecotones are transition zones where spatial changes are more rapid within the zone than in the adjoining areas (Holland 1988; Risser 1995); these transition zones may or may not have unique properties or landscape level consequences (Hood et al. 2003; Walker et al. 2003). Patch dynamics refers to changes in ecological properties within and among patches through time (Pickett and Thompson 1978; Pickett and White 1985; Wu and Loucks 1995). By integrating these concepts, we envision 'biotic transitions' (the boundary and the neighboring areas) as consisting of a hierarchy of dynamic patches with different properties, spatial arrangements, and connectivity with other patches that determine the response of the transition zone to a range of environmental conditions. Because boundaries are important from fine to broad spatial scales (Fuentes et al. 2000; Belnap et al. 2003), our goal was to develop an operational framework for transition zones occurring across landscapes that is also applicable to other scales.

In this paper, we first briefly review research on the structure and dynamics of ecotones, boundaries, and patches. Next, we present a conceptual framework of biotic transitions and a series of testable hypotheses that builds on previous ideas to integrate patch dynamics with boundary and ecotone dynamics. Finally, using an arid ecosystem in the Southwestern US, we illustrate how our framework improves our ability to predict landscape responses to changes in environmental drivers.

Ecotones and boundaries

Although ecotones and boundaries have similar properties, they have traditionally been studied from different perspectives. *Ecotones* have primarily been studied by vegetation ecologists interested in dynamics within a transition zone compared to adjacent areas. We adopt a broad definition of an ecotone in time and space, although ecotones with strong temporal fluctuations have been differentiated from ecoclines with clear spatial gradients (van der Maarel 1990). Theoretical frameworks of ecotones developed in the late 1980s and early 1990s (Hansen and di Castri 1992; Risser 1995) included a hierarchy of spatial scales (Gosz 1993), however most research continues to focus on ecotones either between ecosystem types, such as forest-agricultural field edges (Weathers et al. 2001), or between biomes (Gosz 1993; Kröel Dulay et al. 2004). Effects of edaphic factors and biological processes on ecotone location and dynamics have been examined (e.g., Montaña et al. 1990; Peters 2000), and methods have been developed to detect ecotone location (e.g., Milne et al. 1996; Fagan et al. 2003). Research has also been conducted on the underlying mechanisms related to shifts in ecotone location and composition through time and across space, such as alpine-treeline ecotones (Körner 1998; Jobbágy and Jackson 2000). Different types of ecotones have been differentiated based on their origin as well as their dynamics (Wu and Archer 2005).

Boundaries or edges have typically been examined with a focus on the properties of a boundary that influence the rate and pattern of movement of organisms, matter, and energy between adjacent areas or habitats (Wiens et al. 1985; Lidicker 1999; Puth and Wilson 2001; Wiens 2002). Boundaries have been classified based on the mechanisms through which edges alter species interactions (Fagan et al. 1999). In some cases, boundaries and ecotones are viewed as synonymous: both have important effects on movement of animals and materials, rates of nutrient cycling, and levels of biodiversity (Shaw and Harte 2001; Weathers et al. 2001; Cadenasso et al. 2003; Hood et al 2003; Seastedt et al. 2004).

It is often assumed that ecotones and boundaries have a specified structure, composition, and location. Less attention has been directed to understanding the relationship between the structural properties of the transitional area and its dynamics through time and across space. Recent studies provide support for the presence of dynamic patches within transitional areas (Archer et al. 1988; Barnes and Archer 1996; Allen and Breshears 1998; Peñuelas and Boada 2003; Alftine and Malanson 2004; Mast and Wolf 2004) and the

influence of patch pattern on responses of ecotones to environmental change (Malanson et al. 2001). However, a conceptual framework is needed to explain these structure-dynamics relationships for different types of ecotones and boundaries. For clarity, we use the term boundary as a general term throughout the rest of this paper.

Patch properties and dynamics

A patch is a relatively discrete, bounded area of any spatial scale that differs from its surroundings in its biotic and abiotic structure and composition (Pickett and Cadenasso 1995). Patches can be created by disturbance agents or by edaphic conditions and microclimate (Pickett and White 1985). Following patch creation, internal patch dynamics are governed by within-patch successional processes and interactions among different patches and with the surrounding matrix. These interactions result in the growth, expansion, and loss of a patch through time (Watt 1947). At a broader spatial scale, a shifting mosaic of patches exists, each at its own successional stage (Bormann and Likens 1979). The spatial distribution of patches at this broader scale may or may not be in equilibrium through time. Patch dynamics theory has been integrated with hierarchy theory to relate pattern, process, and scale within the context of landscapes (Wu and Loucks 1995; Wu 1999). We further expand these ideas to include boundary dynamics.

Although a number of patch properties can be important to patch dynamics, we focus on size, type, spatial configuration, and connectivity as key properties that influence the function and dynamics of biotic transitions. Patch size has affects on within-patch processes, such as nitrogen cycling and recruitment (Ludwig et al. 2000), and processes that connect patches, such as animal movement (McIntyre and Wiens 1999). Patch type is defined by the composition and abundance of fine-scale entities within the patch, and is typically determined by the entities with the highest proportion of cover that dominate patch function. Spatial configuration refers to the distribution of patches, and includes measures of richness, evenness, and dispersion (Wiens et al. 1993). Connectivity includes the functional relationships among patches as a result of spatial properties of the

landscape and movement of organisms in response to landscape structure (With et al. 1997, 1999).

Biotic transitions: a conceptual framework

In our conceptual framework, we use the theory of patch dynamics to describe and understand the structural properties of biotic transitions, and to predict changes in boundaries through time and across space. Although our framework is applicable at both finer (e.g., leaf or root) and broader scales (e.g., region or biome), we focus on a hierarchy of spatial scales relevant to landscape dynamics: (1) individuals, (2) assemblages of species, and (3) species associations (Kotliar and Wiens 1990; Wu and Loucks 1995). At the scale of individual plants, for example, root and canopy patches exist in the boundary between neighboring plants that affect competition for resources and individual plant success (Belnap et al. 2003; Figure 1a). Boundaries between adjacent assemblages or groups of plants of similar or different species consist of individual plant and interspace patches (Figure 1b). Adjacent associations or plant communities have boundaries (i.e., ecotones) consisting of groups of assemblages of plant patches that influence species distributions (Figure 1c). Landscapes consist of a mosaic of associations, patches and their boundaries (Figure 1d). At all scales, our interest is in the spatial distribution of biotic entities (patches) through time, and how interactions among these entities influence boundary dynamics across the biotic transition. We are particularly interested in patches defined by the dominant plant species that can influence boundary dynamics for the system. Although we focus on multiple spatial scales, we recognize the relationship between spatial and temporal processes.

By our definition, a biotic transition consists of three neighboring spatial states that differ in the aggregation and connectedness of their sub-units or patches (Figure 1). Each state is defined on the basis of the abundance, spatial distribution, and connectivity of patches of the same or different type. The two states on either side of the boundary ('end states') are homogeneous and consist of highly aggregated and well-connected patches of the same type. Because these patches are highly connected, the average property of these end states
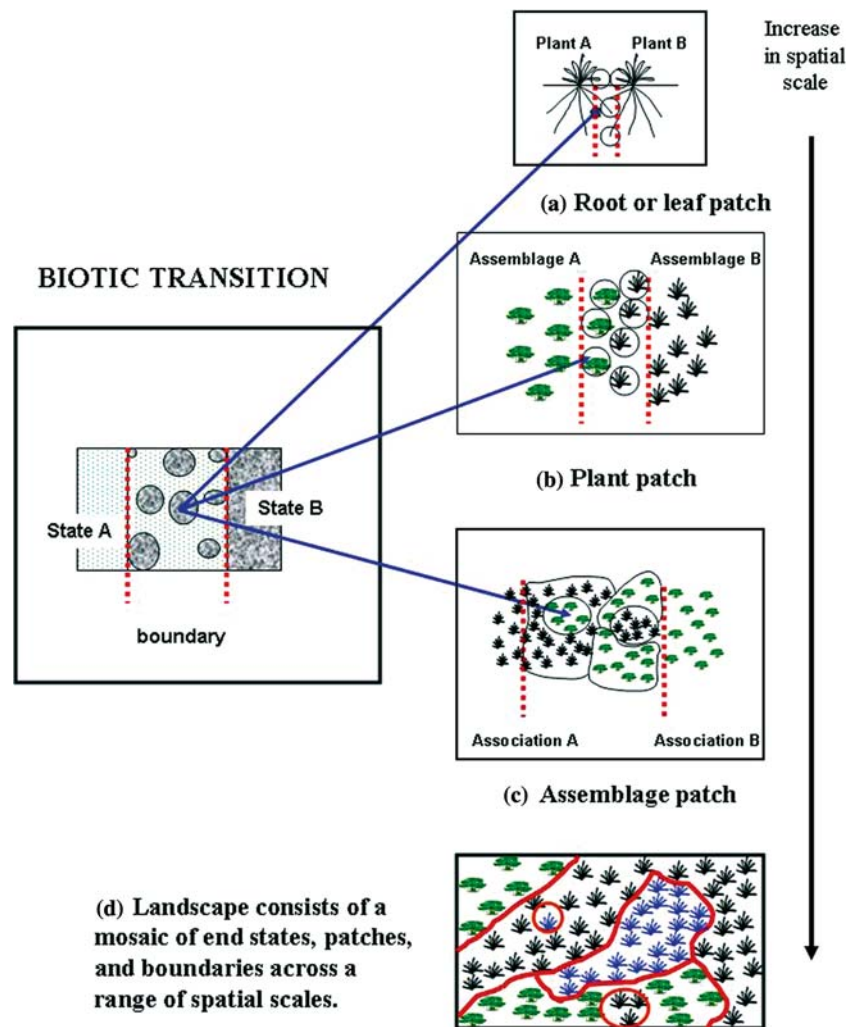
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Figure 1. Conceptual framework of biotic transitions at multiple spatial scales. A biotic transition consists of two end states (A, B) with a boundary between them. Patches within the end states (not shown) are highly aggregated and well connected. The boundary consists of patches from both end states that vary in size, type, spatial configuration, and degree of connectivity. The framework is applicable across a range of spatial scales, for example: (a) individual plants where the boundary consists of root or leaf patches from each plant, (b) assemblages of plants where the boundary consists of patches of individual plants of one species interacting with plants of a different species from an adjacent patch, (c) associations or groups of plant assemblages where each assemblage dominated by one species is a patch, and the boundary consists of these interacting groups of plants, and (d) the landscape that consists of a mosaic of boundaries and end states at all smaller scales. At this broad scale, boundaries often appear as edges.

can be linearly extrapolated from the properties of the patches. Patches representing different end states occur infrequently within this end state and do not contribute significantly to its overall dynamics, particularly with regard to boundary conditions.

The third spatial unit or 'boundary' between end states consists of disaggregated patches of different types with large differences in patch properties and variable connectivity; this heterogeneity in patch properties and distribution results in nonlinear rates of ecological flows across the spatial extent of the boundary. Boundary dynamics depend on properties of patches and biological processes (e.g., colonization, establishment, species interactions) interacting with the environmental template to create new patches, maintain and coalesce current patches, and lose patches through time. Spatially, the location of a boundary as well as the spatial distribution of end states can change

through time depending on the balance between the increase in number and cover of patches of the same type (initiation, growth, coalescence) with the decrease in abundance of that patch type within the boundary (patch loss).

Properties of biotic transitions

A major challenge when studying transition areas is to determine the location of a boundary. Most edge detection techniques assume that the existence of a discontinuity in vegetation structure determines boundary location (e.g., Milne et al. 1996), and some techniques consider dynamic modeling of boundaries (Fagan et al. 2003). However, the heterogeneous nature of vegetation often leads to difficulties in identifying boundary location, especially as the spatial grain and extent change (Walker et al. 2003).

Our patch dynamics conceptualization provides an approach to determine the location of boundaries based on patch structural properties (size, type, spatial configuration, connectivity) that are hypothesized to be related to boundary dynamics. Because patch size is often a covariate in explaining patch behavior and response, other characteristics are considered in the context of a range of patch sizes. As the abundance and cover of patches within a boundary increase, they tend to coalesce into larger patches. As patch size increases, we hypothesize that processes and characteristics of a patch become more similar to the properties of the homogeneous end state dominated by patches of the same type. After a patch reaches a certain size, it functions similar to the end state dominated by the same patch type, and the boundary effectively changes location to include this large patch as part of the end state (Figure 2). Thus, boundary location can be identified as the location on the landscape where the dynamic attributes of the patches
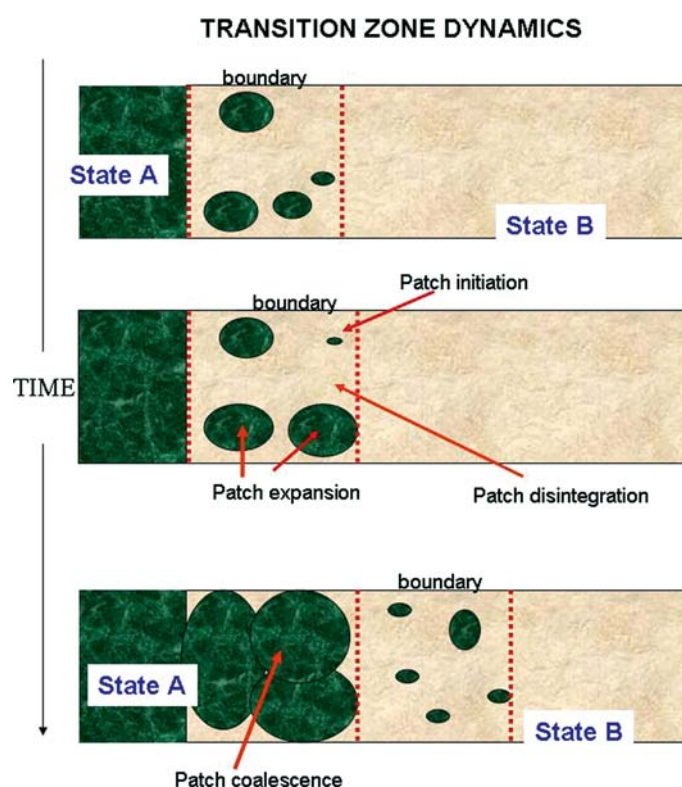

Figure 2. Patch dynamics of initiation, expansion, coalescence, and disintegration occur within a biotic transition to shift the boundary location through time. The boundary consists of dark discrete patches representing end state A within light areas representing end state B. Through time, the patches of end state A grow larger and more abundant, thus coalescing and shifting the location of A as well as the boundary between A and B. Patches of end state B can also occur within end state A, but are not shown.

become similar to the end state. Because the relationship between patch size and similarity to the end state is expected to differ between types of processes and patch types, boundary location is also expected to depend on the process studied.

In addition, we hypothesize that connectivity by plants and animals among patches of the same type increases with patch size until the aggregated patch is sufficiently large that it functions similar to the end state. For example, small patches, such as isolated shrubs located in large patches of grassland, may not be used by small animals as forage because insufficient cover increases the risk of predation (Sanchez and Parmenter 2002). Thus, from the perspective of small mammals, these isolated patches have low connectivity. Once a patch consists of a larger group of shrubs, then the combined cover may be sufficient for animals to risk moving to that patch, thus increasing the connectivity of patches.

Biotic transition dynamics

We identify three types of transitions (directional, stationary, shifting) that are differentiated by their patch and boundary characteristics and dynamics as well as the key drivers and constraints influencing these dynamics (Table 1). These types of transitions differ in the relative importance of four interacting factors: (1) abiotic drivers (e.g., climate), (2) biotic feedback mechanisms (e.g., competition), (3) inherent abiotic constraints (e.g., geomorphology), and (4) dynamic abiotic feedback mechanisms (e.g., organic matter accumulation). Abiotic drivers have temporal variation that influences the system, but are not influenced by the system; these drivers are most important for directional and shifting transitions. Biotic feedback mechanisms occur between the vegetation,

Table 1. Three types of biotic transitions and the strength of abiotic constraints, biotic and abiotic feedbacks.

Biotic transition	Abiotic drivers	Biotic feedbacks	Inherent abiotic constraints	Dynamic abiotic feedbacks
Directional	Strong	Strong	Weak	Strong
Stationary	Weak	Strong	Strong	Negligible
Shifting	Strong	Weak	Weak	Weak

animals, and soil biota to influence future ecosystem dynamics, in particular for directional and stationary transitions. Inherent abiotic constraints refer to properties, such as parent material, which change little through ecological time; these constraints are most important for stationary transitions. Dynamic abiotic feedback mechanisms refer to community-induced changes in microclimate or dynamic soil properties, such as the amount of organic matter, which influence future community dynamics, particularly for directional transitions.

Although these types of biotic transitions occur at all spatial scales, we illustrate our framework using species associations and their corresponding patch dynamics.

Directional transitions

Directional transitions involve the movement or invasion by patches from one end state into another end state. Thus, the location of the boundary between the two states moves uni-directionally through time, although the rate may be variable. Well-known examples include the invasion by exotic herbaceous species and the encroachment of native woody plants into perennial grasslands (Archer et al. 1988; Mack et al. 2000). These biotic transitions are similar to positive feedback switches (Wilson and Agnew 1992).

Directional transitions are strongly influenced by abiotic drivers and biotic and abiotic feedback mechanisms, and initially, a strong abiotic constraint that weakens with time. For example, abiotic drivers have important influences on the establishment of individual plants causing the initiation of patches. Spatial variation in soil properties (i.e., abiotic constraints) provides a heterogeneous template for successful recruitment. Following patch initiation, both positive biotic and strong abiotic feedback mechanisms act to promote the maintenance of the invader patch through time (Montaña et al. 1990; Schlesinger et al. 1990). Positive feedback mechanisms also affect patch expansion and coalescence through the increased probability of recruitment of new individuals within the patch as its size increases. Strong biotic feedback mechanisms, such as by animal movement, lead to increasing connectivity of patches as distance between patches decreases. Patch size is expected to be largest near its own

end state where patches have had time to coalesce, and decrease as distance from the end state increases, as predicted by models of ecotones (Neilson 1993).

Stationary transitions

Stationary transitions are relatively stable over scales of decades with little movement by patches from one end state into another end state. These environmental boundaries (Lloyd et al. 2000) are controlled by inherent abiotic constraints that are reinforced through time by strong biotic feedbacks (Weltzin and McPherson 1999). Thus, patch initiation, expansion, and coalescence are controlled by the abiotic environment; suitable conditions for these processes do not occur outside the boundary (Schauer et al. 1998). Although the boundary often appears as an 'edge', small fluctuations in its location can occur through time due to climatic fluctuations. Abiotic drivers have weak effects and the effects of abiotic feedbacks between vegetation and dynamic soil properties, for example, are negligible. Stationary transitions are most common along abrupt elevational or geomorphic gradients where major changes in climate or soils result in changes in vegetation (Körner 1998) or as a result of human activities. Disturbances within a boundary can result in short-term changes in species composition, but successional dynamics result in a return to the abiotically controlled community (Noble 1993).

Shifting transitions

Shifting transitions involve no net change in the location of a boundary over relatively long periods of time (e.g., decades). However, favorable conditions for one end state can allow the movement or increase of its patch types across the boundary for a period of time; conditions that favor patch types from another end state can allow its spread in the boundary during other time periods. The initiation, expansion, coalescence, and disintegration of patches are strongly affected by abiotic drivers that are not reinforced through time, either by positive biotic or abiotic feedback mechanisms, or by abiotic constraints. The patches are dynamic through time and space, and generate a shifting mosaic of patches within the boundary. An example is the differential responses to fire, grazing, and precipitation by perennial grasses in semiarid grasslands that result in shifts in dominance as the drivers fluctuate through time (Weaver and Albertson 1943; Gosz and Gosz 1996). Because shifting transitions may appear to be directional at fine temporal scales, long-term studies are often needed to document these dynamics.

Landscape dynamics

Landscape dynamics depend on the mosaic of types of transitions contained within the landscape. Thus, determining the type of transition for each boundary within a landscape is a critical step in predicting the response of the landscape to environmental drivers. Landscape consisting primarily of stationary transitions will be relatively stable through time regardless of changes in environmental drivers. By contrast, landscapes consisting primarily of directional transitions will respond to favorable landuse or climatic conditions, and this expansion will be maintained through time even if the environmental conditions become unfavorable. Landscapes consisting of shifting transitions will also respond to changes in climate or landuse, but these changes are reversible when the environmental conditions change.

In two of these transition types, directional and shifting, patch dynamics result from species interactions at patch boundaries, not just from successional changes within the patch as is often described in studies of patch dynamics (Watt 1947). Therefore, in many systems, landscape dynamics result from the interplay of internal patch dynamics and boundary dynamics. Moreover, in cases where boundaries shift back and forth over time, point diversity will be relatively high compared to stable areas within patches, as species in the boundary zone appear and disappear over time.

A case study from the Sevilleta National Wildlife Refuge

Arid and semiarid landscapes at the Sevilleta National Wildlife Refuge in central New Mexico,

USA provide support for our framework and illustrate its utility in understanding and predicting landscape dynamics. Climatically-controlled biomes meet at the Sevilleta to form transitions across a range of spatial scales. The shortgrass steppe biome located along the Front Range of the Rocky Mountains is dominated by the C_4 long-lived (> 100 years) perennial grass, blue grama (*Bouteloua gracilis*). The Chihuahuan Desert biome of central and southern New Mexico and north-central Mexico is often differentiated into two vegetation formations: Chihuahuan Desert grasslands dominated by the short-lived (25–40 years) C_4 perennial grass, black grama (*Bouteloua eriopoda*), and Chihuahuan Desert shrublands dominated by long-lived (> 100 years) C_3 shrubs, including creosotebush (*Larrea tridentata*). Other species of C_3 and C_4 annual and perennial grasses, forbs, subshrubs, and shrubs as well as succulents occur throughout the Sevilleta landscape. For purposes of illustration, we focus on biotic transitions formed by interactions among the three dominant species.

Transitions between blue grama, black grama, and creosotebush occur across a range of spatial scales (Figure 3). Because water is the most frequently limiting resource in arid and semiarid ecosystems, individual plants of each species often compete for soil water such that boundaries between neighboring plants consist of root patches that correspond to soil resource patches (Figure 3a). At a larger spatial scale, groups or assemblages of black grama plants often form boundaries with adjacent groups of creosotebush plants (Figure 3b) or blue grama plants (not shown). Intraspecific interactions between plants dominate the interiors of the assemblages whereas intra- and interspecific interactions among plants are important at boundaries. At a larger scale, associations or communities consist of groups of plant assemblages of variable size, connectivity, and spatial arrangement that are dominated by one of the three species (Figure 3c). Landscapes consist of a mosaic of biotic transitions that includes all finer spatial scales (Figure 3d).

Our recent research indicates that all three types of transition dynamics (directional, stationary, shifting) can be found even when only considering patterns in blue grama, black grama, and creosotebush dominance. However, the frequency of occurrence of these transitions varies by species combination. Transitions occur most frequently between creosotebush and black grama or between black grama and blue grama; transitions between creosotebush and blue grama occur infrequently (Figure 4). Our framework provides insight into these spatially variable patterns in species combinations as related to transitions, and can be used to improve understanding and predictions of landscape dynamics.

Directional transitions

Directional transitions at the Sevilleta occur primarily as a result of the expansion of the native creosotebush into perennial grasslands. Creosotebush currently dominates thin, rocky soils; however patches of variable size and age can be found expanding primarily within black grama grasslands on loamy soils (Peters et al. submitted). Based on our framework, we expect that increases in creosotebush patch sizes through time are strongly affected by positive feedbacks between shrubs and their microenvironment that change in strength as creosotebush patches change in size. Results from large associations of creosote plants support the importance of these feedbacks: enhanced overland flow, soil erosion, and nutrient redistribution occur as a result of plant-soil feedbacks in creosote dominated communities (Lyford and Oashu 1969; Abrahams et al. 1995; Kieft et al. 1998; Schlesinger et al. 2000; Bhark and Small 2003).

We expect that these feedback processes are also important in maintaining creosote-dominated patches, but only after a patch reaches a certain size. Negative effects of shrubs on perennial grass seed viability and presence of seeds in the soil (Peters 2002b) may reduce grass abundance and further promote the expansion of shrub patches. Associated changes in rodent and arthropod assemblages with shrub invasion (Sanchez and Parmenter 2002) may also negatively impact grasses through herbivory of seedlings and adults. These positive and negative feedback mechanisms associated with shrubs and grasses, respectively, are expected to result in a nonlinear increase in patch size and aggregation of shrubs with a nonlinear shift in the location of a boundary through time as the geographic distribution of shrubs
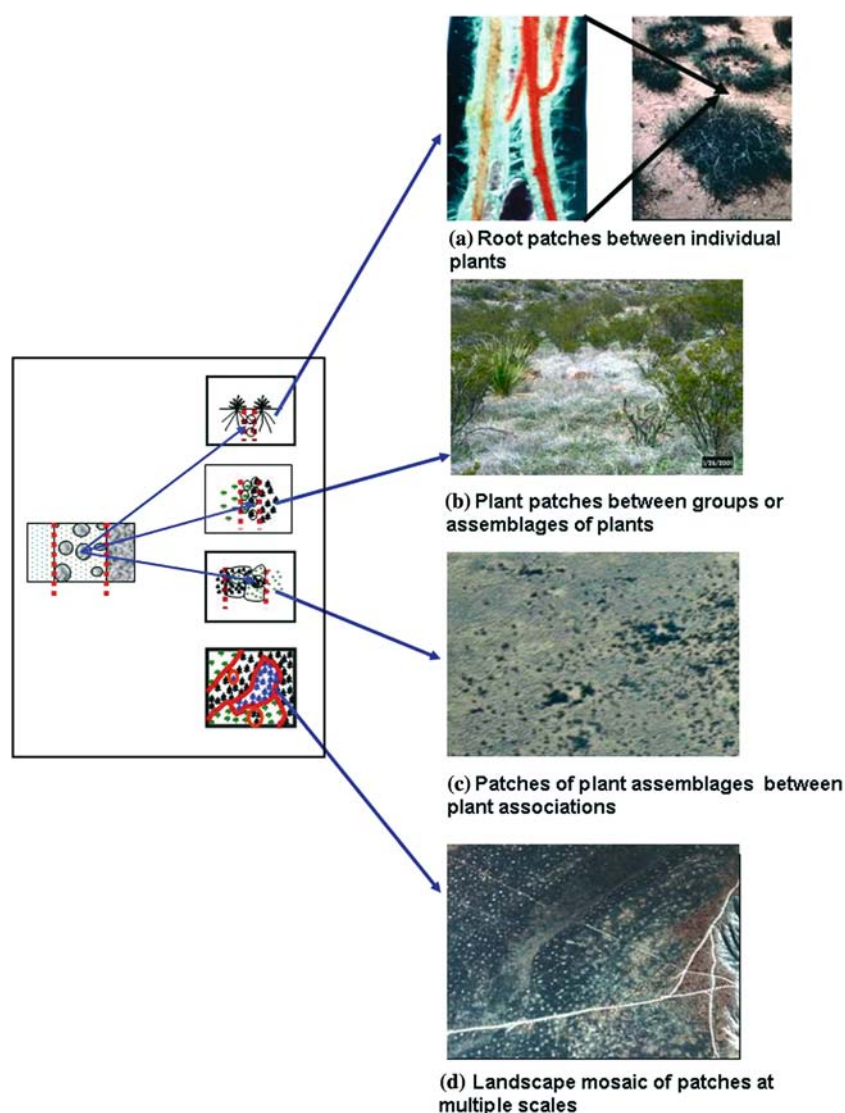
Figure 3. Illustration of our conceptual framework across a range of spatial scales for the Sevilleta site in central New Mexico. The schematic on the left is our general framework (Figure 1) showing biotic transitions consisting of two end states and the intervening boundary. Boundaries are highlighted in red. The arrows point to the corresponding scale for the Sevilleta: (a) on the right are root patches that occur between individual plants of blue grama (background) and black grama (foreground). On the left are individual roots illustrated using black grama (yellow) and a semiarid shrub, *Atriplex caniscens* (red). (b) Patches of individual plants of a grass (black grama) and a shrub (creosotebush) comprise groups or assemblages of plants (photo from Big Bend National Park). (c) Patches of creosotebush assemblages (dark) are shown as a mosaic of patches of different sizes and distances from the end state dominated by creosotebush to the right of the photo. The light colored matrix is a mosaic of homogeneous and highly connected grass patches. (d) The landscape consists of a mosaic of patches at multiple spatial scales. Creosotebush is shown in brown, black grama is black, and blue grama is light colored. The small white dots in (d) are bannertail kangaroo rat mounds.

increases. Such nonlinear invasion rates and changes in aggregation of shrub patches and boundaries have been observed in grassland eco-systems worldwide (Schlesinger et al. 1990; Archer et al. 1998; Goslee et al. 2002; Peters et al. 2004).

Stationary transitions

Stationary transitions at the Sevilleta occur most often between blue grama and black grama dom-inated areas on different soils (Figure 4b) (D.P.C.
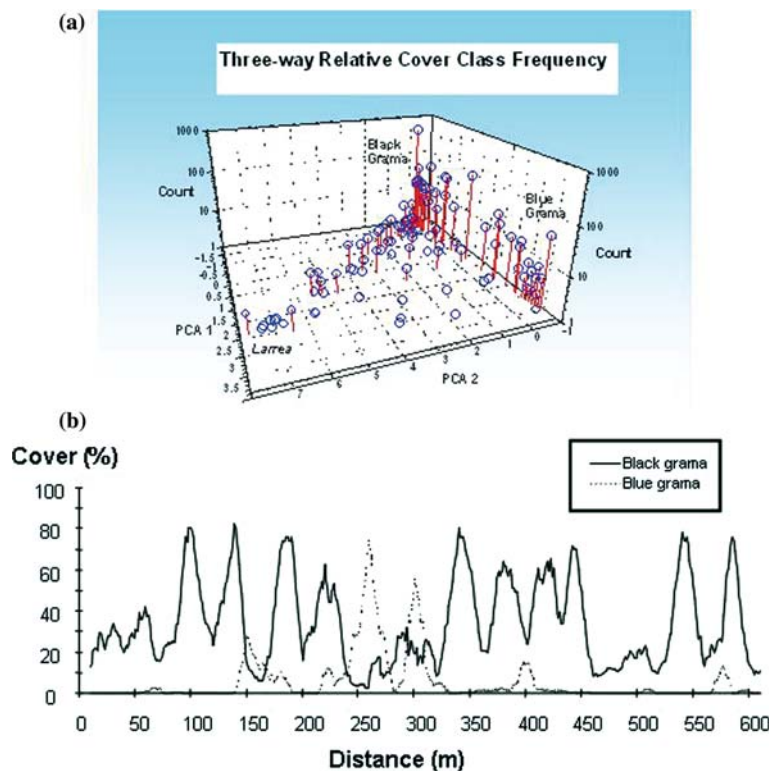
Figure 4. (a) Principal components analysis of relative cover among creosotebush (*Larrea*), black grama, and blue grama in 1522 100 m^2 quadrats along three belt transects on McKenzie Flats at the Sevilleta. PCA 1 represents the gradient between black grama to blue grama, and PCA2 is the gradient between the two grass species and creosotebush. The *z* axis is the number of counts for a given combination of covers. (b) The running mean cover of black grama and blue grama in 100 m blocks from south to north along the western 6 km belt transect. The sharp boundaries at 240 and 275 m suggest a stationary transition whereas mixed communities of blue grama and black grama at 150 and 170 m, and again at 290 and 325 m are indicative of shifting transitions.

Peters unpublished data). Based on our framework, we expect that these transitions are primarily controlled by soil texture constraints and water availability interacting with plant life history traits to generate stable vegetation patterns through time. Although there is a large overlap in the soils where each grass species can dominate, only blue grama grasslands are found on sites with high clay and low sand content with greater depth to calcium carbonate; black grama grasslands are found on sites with high sand content, and shallower, less developed soils (Buxbaum 2003; Kröel Dulay et al. 2004). Differences between grass species in traits related to soil water availability, such as rooting distribution, recruitment potential, and drought tolerance, are expected to result in these vegetation patterns.

Because of the strong inherent abiotic constraints and biotic feedback mechanisms, these patterns persist through time even in the presence of environmental drivers that differentially impact the two species. For example, over the past 20 years following the removal of livestock grazing that more severely impacts black grama, blue grama grasslands have persisted on sites with fine textured soils and black grama grasslands persisted on coarser soils (Ryerson and Parmenter 2001). Although these broad scale patterns are persistent, factors that result in fine scale mortality of one species by disrupting the plant-soil feedback mechanisms can shift dominance at finer scales. For example, digging activities of banner-tail kangaroo rats allow black grama dominance in areas surrounding mounds, even in blue grama-dominated grasslands (Fields et al. 1999). In this case, directional transitions occurring at a fine scale between blue grama and black grama assemblages around kangaroo rat mounds are

imbedded within larger scale stationary transitions between associations dominated by each species. It is only possible to disentangle these complex spatial and temporal patterns by examining patch and boundary dynamics at multiple scales.

Shifting transitions

Shifting transitions occur at the Sevilleta between blue grama and black grama grasslands located on soils with intermediate sand and clay contents (Figure 4b). Based on our framework, shifts in dominance and species composition are expected to be related to changes in the climatic or disturbance regime (e.g., fire, grazing) that favor one species over another. With a return to the previous climate or recovery from disturbance, the previous vegetation type once again dominates. Changes in drivers do not persist sufficiently long to remove species from the regional pool; thus a return to dominance by the previous species is possible when previous conditions return. Positive feedback mechanisms between plants, soils, and animals are weak, and do not reinforce the vegetation patterns through time. Decade-long data document this shifting mosaic between blue grama and black grama at the Sevilleta (Anand and Li 2001). Severe decadal drought cycles (Milne et al. 2003) likely contribute to this shifting mosaic. However, a directional change in a driver may generate long-term changes in boundary location and composition that over time would change a shifting transition to a directional one (Peters 2002a).

Landscapes

Landscapes at the Sevilleta consist of a mosaic of different types of transitions, mostly between the three dominant species (blue grama, black grama, creosotebush). The density, spatial extent, and spatial arrangement of these transitions are expected to be important to landscape scale dynamics (Peters et al. submitted). Although most of the study site is dominated by perennial grasslands, creosotebush and other shrubs have expanded extensively throughout the Southwestern United States (Grover and Musick 1990). The continued dominance by grasslands at the Sevilleta despite region-wide shrub expansion can be explained using our framework where landscapes consist of different types of transitions. Stationary transitions between blue grama and black grama dominated communities combined with the low invasibility of creosotebush into blue grama dominated communities suggests that it is the location and density of these types of transitions that limit the ability of creosotebush to directionally expand across the Sevilleta landscape.

New insights arising from our framework

Our conceptual framework provides an approach to disentangling landscape complexity. For example, at the Sevilleta, landscape patterns and dynamics are not always predictably related to environmental variables, such as soil texture, historic disturbance, or short-term fluctuations in precipitation (Anand and Li 2001; Ryerson and Parmenter 2001; Kröel-Dulay et al. 2004). It is only by applying our new conceptual framework that integrates patch dynamics with boundary dynamics that we can understand controls on species distribution, abundance and interactions in these landscapes, particularly under conditions of changing climate and land use. For example, some transitions between blue grama and black grama communities shift back and forth spatially through time as precipitation and grazing management change whereas other transitions between these same communities are stationary over the same time period. Previous to implementation of our conceptual framework, it was possible to view, and thus sample, these very different transitions as replicates. Using our new framework that focuses on underlying constraints as well as dynamics of transitions is critical to disentangling these complex landscapes in order to understand past dynamics and to predict future changes in patch structure and boundary location.

Furthermore, we urge caution when extrapolating boundary dynamics to apparently similar situations. Vegetation structure based on species dominance without regard to patch structure and underlying constraints may be insufficient to understand boundary dynamics. Differences in patch structure are key boundary characteristics that can be used to identify these different transitions; broad boundaries with a mosaic of patches dominated by different species are more likely to

be shifting transitions whereas sharp boundaries between patches of each species are more likely to be stationary through time. Preliminary data support these patterns in patch structure and configuration with links to boundary dynamics at the Sevilleta (D.P.C. Peters unpublished data). Our approach provides guidance in identifying the processes and constraints on boundary dynamics, in stratifying the landscape based on transitions expected to display different dynamics, and in identifying the location of boundaries based on structural attributes.

Patch structure and development have been used previously to infer changes in boundary dynamics between forests and grasslands with changes in climate and land use (Mast and Wolf 2004). The rapid response of boundaries to extreme climatic events also involves patch dynamics and properties of forest fragments remaining after broad scale, yet incomplete mortality of trees (Allen and Breshears 1998). Woody plant encroachment into perennial grasslands has been conceptualized using patch dynamics (Barnes and Archer 1999) and alpine tree line relationships also involve patch patterns and dynamics (Alftine and Malanson 2004). Our approach provides a general framework for these different studies, and allows us to make predictions about boundary dynamics based on patch structure and dynamics combined with underlying environmental constraints and feedback mechanisms.

Summary and conclusions

Biotic transitions (two end states and the boundary between them) are a common feature of landscapes. Although we illustrated our conceptual framework with vegetation examples from semiarid and arid ecosystems, our framework linking theories of patch and boundary dynamics at multiple scales applies to other systems. For example, forest communities include tree-to-tree interactions governing species replacement patterns (e.g., Figure 1a). At larger scales, boundary interactions between canopy gaps and undisturbed forest affect the rate of change in species composition within gaps (Figure 1b). Within forest stands, the population of different aged canopy gaps and their boundaries create a shifting mosaic of patches and undisturbed forest (Figure 1c).

Finally, landscapes contain complex mosaics of forest, field, and wetland patches with multiple types of boundary interactions (Figure 1d). In all cases, there is a hierarchical set of interactions across boundaries that are influenced by patch properties and dynamics. Thus, our conceptual framework can be applied to multi-scale interactions in different types of ecosystems.

Historically, boundaries have been mostly viewed as relatively stable zones of vegetation with differential effects on movements of animals, plants, and materials. Our conceptual framework places a distinct emphasis on the properties of boundaries that influence their dynamics within the context of the broader biotic transition. Moreover, our framework emphasizes the role of boundary dynamics, in addition to patch dynamics, as a key driver of landscape change. The framework accommodates the responses of gradual and sharp transition zones as well as different types of boundaries (Fagan et al. 1999; Lloyd et al. 2000). Essentially, we envision landscapes as dynamic systems of patches that are coalescing or disintegrating primarily through the expansion, fluctuation or erosion of boundaries through time. Although some boundaries may be relatively stable in ecological time, in other cases, interactions within biotic transitions will result in landscapes characterized by fluctuations in the number, type and size of patches, along with directional shifts from one patch type to another in response to local and regional drivers. Thus, our framework places increasing emphasis on the dynamics of boundaries and their role in driving patch dynamics and landscape change.

As the human population further modifies the biosphere, landscape structure will become increasingly more complicated with the addition of distinct patches with well-defined boundaries to patches characterized by gradual environmental change. As a result, biotic transitions with different types of dynamics will occupy an increasingly larger proportion of the landscape through time. Such dramatic changes in landscape structure will have significant consequences for ecological properties and processes ranging from biodiversity to biogeochemistry. Thus, a conceptual framework that includes different types of biotic transitions that is applicable across a range of scales, such as the one we propose, is needed to improve understanding and prediction about how future

landscapes will respond to human-driven and natural changes in climate and land-use.

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