SOIL-GEOMORPHIC HETEROGENEITY GOVERNS PATCHY VEGETATION DYNAMICS AT AN ARID ECOTONE

Brandon T. Bestelmeyer,[1] Judy P. Ward, and Kris M. Havstad

*USDA-ARS, Jornada Experimental Range and Jornada Basin LTER, MSC 3JER, Box 30003, New Mexico State University,
Las Cruces, New Mexico 88003 USA*

Abstract. Soil properties are well known to affect vegetation, but the role of soil heterogeneity in the patterning of vegetation dynamics is poorly documented. We asked whether the location of an ecotone separating grass-dominated and sparsely vegetated areas reflected only historical variation in degradation or was related to variation in inherent soil properties. We then asked whether changes in the cover and spatial organization of vegetated and bare patches assessed using repeat aerial photography reflected self-organizing dynamics unrelated to soil variation or the stable patterning of soil variation. We found that the present-day ecotone was related to a shift from more weakly to more strongly developed soils. Parts of the ecotone were stable over a 60-year period, but shifts between bare and vegetated states, as well as persistently vegetated and bare states, occurred largely in small (<40 m^2) patches throughout the study area. The probability that patches were presently vegetated or bare, as well as the probability that vegetation persisted and/or established over the 60-year period, was negatively related to surface calcium carbonate and positively related to subsurface clay content. Thus, only a fraction of the landscape was susceptible to vegetation change, and the sparsely vegetated area probably featured a higher frequency of susceptible soil patches. Patch dynamics and self-organizing processes can be constrained by subtle (and often unrecognized) soil heterogeneity.

Key words: autocorrelation; Chihuahuan Desert; patch dynamics; rangeland; self-organization; state-and-transition model; threshold.

INTRODUCTION

The mechanisms underlying the formation of alternative stable states expressed as two-phase patch mosaics (i.e., vegetation pattern) have become a major focus of research in the ecology of rangelands (Aguiar and Sala 1999, Tongway et al. 2001, Rietkerk et al. 2004). Arid, semiarid and subtropical grassland grazing systems around the world have undergone irreversible (or catastrophic) transitions from grass-dominated mosaics to largely bare or shrub-dominated ones with several negative consequences (Reynolds and Stafford Smith 2002). In some grassland areas, however, transitions have not occurred, even in areas adjacent to degrading grasslands (Gibbens et al. 2005). Despite recent theoretical efforts to explain the mechanisms underlying catastrophic transitions (van de Koppel and Rietkerk 2004) and variation in ecosystem resilience (Gunderson 2000), we continue to have a poor understanding of the factors determining the spatial pattern of vegetation and its resilience over time.

Theoretical explanations for catastrophic transitions in grasslands emphasize the role of variation in climate and grazing pressure (e.g., along landscape gradients) in

the demography of plants and subsequent effects on soils (e.g., Friedel 1991). Under heavy grazing pressure palatable grasses die while unpalatable woody plants undamaged by grazing often persist (Archer et al. 1988). In the absence of grasses, reduced infiltration rates and nutrient cycling preclude conditions necessary for the reestablishment of grasses (Schlesinger et al. 1990). Beyond a certain level of disturbance-induced grass loss, the positive feedback system favoring grassland can be irreversibly damaged.

Recent elaborations of this theory have shown that fine-scale patch-dynamic processes may generate broad-scale spatial patterning in vegetation (HilleRisLambers et al. 2001). At sufficiently high levels of grass cover, high water capture within the landscape promotes plant growth (Ludwig and Tongway 1997). As cover declines with disturbance and bare ground connectivity increases, the reduced rate of resource capture accelerates vegetation decline (Davenport et al. 1998). Spatial transfers of water and sediment from bare patches to remaining vegetated patches may promote system resilience and drive the formation and dynamics of vegetation patterning (e.g., spotted or striped patterns) at broader scales (Aguiar and Sala 1999, Rietkerk et al. 2004, Ludwig et al. 2005). These processes may also result in dynamic ecotones that shift in position over time (Wilson and Agnew 1992, Mauchamp et al. 1993). This "self-organization" model of transitions suggests

PLATE 1. A portion of the sharp ecotone at the Corralitos Ranch, Doña Ana County, New Mexico (USA). The right side of the ecotone (grass side) is dominated by *Pleuraphis mutica*, and the left side (sparse side) features scattered *Flourensia cernua* and *Scleropogon brevifolius*. No evidence was found that a fenceline had ever existed at the site. A color version of this photograph may be viewed in the Appendix. Photo credit: B. Bestelmeyer.

that localized impacts may translate into the broad-scale evolution of vegetation patterns via a suite of endogenous processes (Rietkerk et al. 2004).

Alternatively, vegetation patchiness and system resilience may be governed to varying degrees by extrinsic factors (HilleRisLambers et al. 2001). Spatial heterogeneity in soil properties may be a key factor in many semiarid landscapes (McAuliffe 1994, d'Herbès et al. 2001). Soil properties, including parent texture, soil depth, calcium carbonate accumulation, and argillic horizon development, have strong influences on resources and recruitment strategies available to plants (Hamerlynck et al. 2000, Maestre et al. 2003) and often vary at several spatial scales (Scull et al. 2003). Soil-geomorphic patterns may interact with disturbance to produce stable but fluctuating ecotones (Lloyd et al. 2000). Thus, under the "soil-geomorphic" model, vegetation patterning may reflect the effects of spatially uniform disturbance against a background of preexisting soil heterogeneity. Although previous authors have suggested that self-organizing processes should vary among broad soil classes, soil patchiness occurring within those classes is not viewed as a determinant of vegetation pattern (HilleRisLambers et al. 2001).

There are few empirical studies available that are able to ascertain the degree to which vegetation pattern formation and dynamics are constrained by underlying soil properties and geomorphic context (e.g., Archer

1995, Dunkerley and Brown 2002). Furthermore, the specific soil attributes mediating vegetation change are rarely addressed. Consequently, it is difficult to evaluate the dominant processes giving rise to arid/semiarid vegetation patterns and to use these patterns to interpret processes and derive management applications (Bestelmeyer et al. 2004, Rietkerk et al. 2004). To address this need, we examined an abrupt ecotone separating a relatively continuous grassland from a patchy grassland/shrubland with extensive bare areas. We used a combination of repeat aerial photography and ground observations of vegetation, soil properties, and anthropogenic features. Our first objective was to ascertain whether the ecotone's location reflected only historical variation in degradation (due to the presence of a historical fence line at the boundary with varying grazing management across the fence), or was related to variation in soil and geomorphological properties. Our second objective was to determine whether patches of vegetation and bare ground comprising each side of the ecotone were stable or dynamic, and then ask whether changes in these patches reflected self-organizing dynamics or stable patterns related to soil variation. Self-organizing dynamics would be supported if vegetation change occurred and was unrelated to soil variation (i.e., disturbance or endogenous processes drive the pattern) and not supported if vegetation pattern is simply a static reflection of underlying soil patchiness.
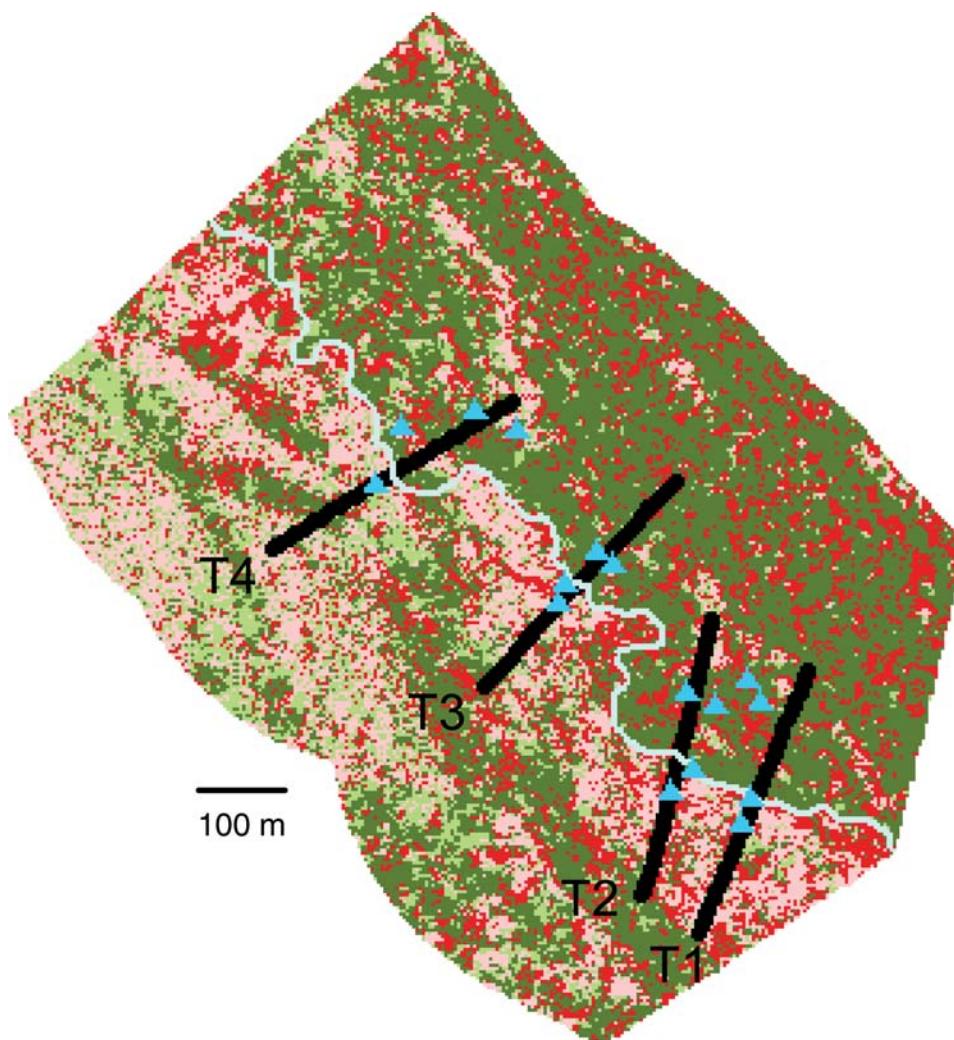
FIG. 1. A map of the study area (Corralitos Ranch, New Mexico, USA) showing patterns of vegetation change from 1936 to 1996 based on image classification of repeat aerial photography: dark green, persistent vegetation (i.e., vegetated in 1936 and 1996); pink, persistent bare ground; red, was vegetated and became bare; light green, was bare and became vegetated. Location of the ecotone (in 1996) is shown by the light blue line. The locations of study transects (black) and soil pits (blue triangles) are shown.

METHODS

Study area

We examined a 62-ha area surrounding an ecotone on the Corralitos Ranch in Doña Ana County, New Mexico, ~25 km east of Las Cruces, New Mexico, USA (see Plate 1). (The coordinate system used was the Universal Transverse Mercator NAD 83, Zone = 13, coordinates 312354 E, 3580730 N.) Mean annual rainfall at the site is 220 mm, but is highly variable from year to year. The study area was defined by manually digitizing the ecotone on a 1996 aerial photograph (U.S. Geological Survey Digital Ortho Quarter Quad; DOQQ) and creating a 300-m buffer around a 1- km linear length of the ecotone (Fig. 1). Dominant perennial grasses in the study area included *Pleuraphis mutica* Buckl., *Muhlenbergia arenacea* (Buckl.), *Scleropogon brevifolius*

Phil., and *Dasyochloa pulchella* (HBK) Hitchc. Shrubs included *Prosopis glandulosa* Torr., *Flourensia cernua* D.C., *Lycium berlandieri* Dunal, and *Larrea tridentata* (DC) Cov.

Current potential grazing pressure is unlikely to differ across the ecotone given the short distances involved and the lack of a fence. The study area was located within a single soil map unit (Berino-Doña Ana association) of the National Cooperative Soil Survey. The two dominant soils constituting this unit were similar and both classified as fine-loamy, mixed, thermic, superactive Typic Calciargids. The ecotone ran parallel to the direction of the slope, which was ~0.5%.

Soil and vegetation measurements

To characterize differences in soil development across the ecotone, we excavated 75 cm deep soil pits in four

representative locations within each of three areas: (1) sparsely vegetated interspaces between shrubs on the sparse side of the ecotone, (2) the ecotone boundary just inside the grass-dominated component, and (3) grass-dominated areas on the grass side of the ecotone. Additionally, we sampled large bare areas on the grass side of the ecotone associated with high rodent activity. Within each pit, the texture, structure, and calcium carbonate content of each morphologically distinguishable soil horizon were evaluated following Soil Survey Staff (1993). Particle-size analysis (PSA) was performed on each horizon using the hydrometer method (Gee and Bauder 1986). The pH for each horizon was determined using an Oakton pHTestr 2, and electrical conductivity (EC) was assessed using an Oakton ECTestr Low (Oakton Instruments, Vernon Hills, Illinois, USA). We used a solution of 1:1 soil to water ratio for both measurements.

To characterize vegetation–soil relationships at particular points in the landscape we established 300 m long transects consisting of 61 points each (5-m spacing) that were geo-referenced perpendicular to the orientation of the ecotone boundary (Fig. 1). The midpoint at 150 m was located on the ecotone boundary (and not considered in subsequent analyses). Transects were spaced randomly along ~1 km of the ecotone. At each point in September–November 2001, we estimated the basal cover of each plant species within each 100-cm^2 cell of a 140 × 140 cm quadrat frame ($N = 196$). In the center of each quadrat, we collected soil samples to a depth of 20 cm at 5-cm increments using a 3.8 cm wide soil auger. This range of depths was chosen because (1) it contains the bulk of the root biomass of desert grasses (Peters 2002, Reynolds et al. 2004) and (2) soil surface textures, particularly those in the top several centimeters, may be critical determinants of infiltration, runoff, and plant establishment in arid environments (Noy-Meir 1973, Graetz and Tongway 1986, Hamerlynck et al. 2000, Maestre et al. 2003). Finally, we used a total station (Pentax PCS-315, Asahi Precision Co., Ltd. Shirako, Wako-shi, Saitama-ken, Japan) to map microtopographic variation among transect points that might be associated with long-term erosion–deposition processes.

Models of vegetation–soil relationships at transect points were focused on soil properties that are predicted to change slowly or not at all relative to land use (Grossman et al. 2001), and that were hypothesized to most directly constrain long-term vegetation dynamics. Other variables (e.g., organic matter content) may change rapidly due to changes to vegetation. Of the selected variables, soil depth and fragment (>2 mm) content were not analyzed because soils were deep (to >3 m in several places we examined) and fragments were absent in most areas. When present, fragments constituted ≤15%. We considered surface silt and clay content, given its importance to water infiltration and retention, and because it is easily lost to erosion (Graetz

and Tongway 1986, Brady and Weil 2002). We considered clay content in the subsoil because it influences rooting patterns and soil water storage (McAuliffe 1994). PSA was performed on all 0–5 cm increments (240 samples) and on a subset of 70 samples for 10–20 cm increments that were randomly selected from points stratified to low (0–1%, 22 points), medium (1–8%, 24 points), and high (8–46%, 24 points) grass cover values.

We also examined calcium carbonate content at the soil surface because it is highly variable and inhibits infiltration (Gile 1961, Hennessy et al. 1983, Gile and Grossman 1997), and because it may limit phosphorus uptake (Lajtha and Schlesinger 1988). Carbonate content was assessed using an effervescence test (Soil Survey Staff 1993). In the laboratory, we applied 0.5 mL of 1 mol/L HCl to ~1 g of the sieved, homogenized soil sample increment. Effervescence was ranked using an interval scale, numbered from 0 (no effervescence) to 4 (violently effervescent). Calcimetry on a subset of 32 scored surface samples using a Scheibler calcimeter (Eijkelkamp Agrisearch BV, Giesbeek, The Netherlands) confirmed that effervescence scores in this study accurately distinguished calcium carbonate equivalent values where a score of $0 = 0$–0.13% of fine-earth mass $CaCO_3$ equivalent, $1 = 0.20$–0.26%, $2 = 0.50$–1.30%, $3 = 1.03$–3.47%, and $4 = 3.57$–6.78%.

Image analysis and relation to field measurements

To assess the magnitude of spatial pattern of change at and around the ecotone, we compared aerial photographs of the study area over a 60-year period from 1936 to 1996. We geo-referenced an aerial photograph encompassing the study area taken in 1936 (Soil Conservation Service, Rio Grande Watershed Project) to the 1996 DOQQ using a second-order polynomial (Root Mean Square Error = 0.0044; cell size = 1 m^2). To compensate for differing optical quality between the two images, we used a texture model with a 61-cell neighborhood standard deviation function (Blom and Daily 1982). Using both the texture model and the original image, we derived 20 classes using an unsupervised classification (IMAGINE 8.7; ERDAS 1999). We reduced these 20 classes to two new classes (bare and vegetated) by comparing individual and contiguous pixels within the classified image to patterns found within the original images.

We characterized the current (2004) status of the vegetation and bare soil cover in each of bare and vegetated classes by sampling 1-m^2 plots representing each class on each side of the ecotone ($N = 80$ for each class). The plot locations were randomly selected, with the criteria for inclusion being that the selected cell existed within a 25-cell neighborhood of identical classification to reduce potential error stemming from positional accuracy in the field. This analysis indicated that cells classified as vegetated had 16.3% ± 1.3% foliar cover of vegetation (mean ± SE), whereas cells classified
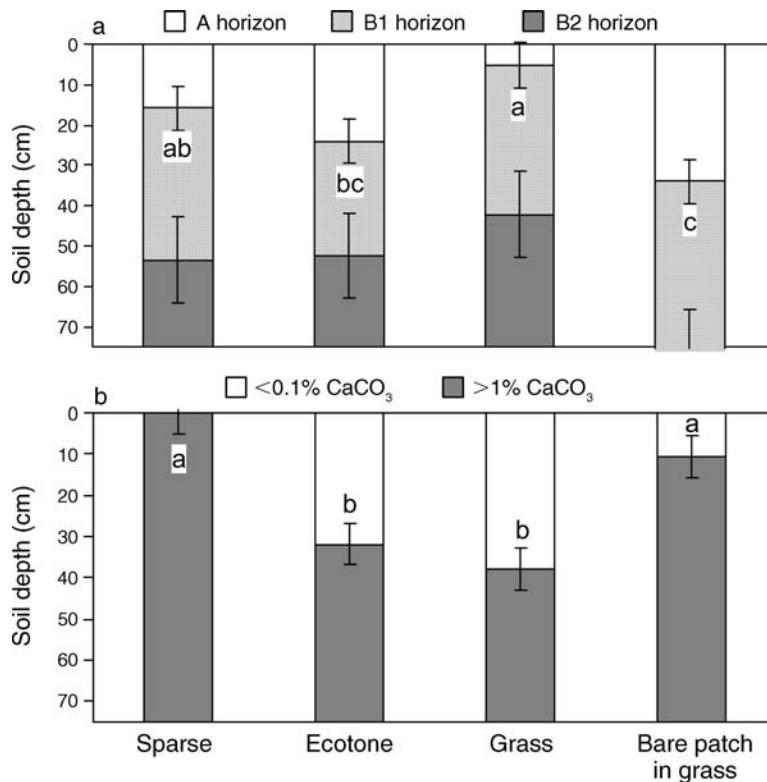
FIG. 2. (a) Mean (±SE) of the depths of contact between the A–B1 and B1–B2 horizons that were differentiated based on soil structure, color, texture, and carbonate and clay accumulation at four pits in each ecotone position. (b) The depth at which calcium carbonate exceeded 1%. Bars with different lowercase letters were significantly different ($P \leq 0.05$).

as bare had $3.8\% \pm 0.5\%$. Thus, we are confident that the image analysis distinguished real patterns.

We overlaid the two classified images to produce an image containing four transitional classes: (1) persistent vegetated, (2) was bare and became vegetated, (3) persistent bare, (4) was vegetated and became bare (ARC/INFO 9.0; ESRI 1995). Landscape metrics (percentage of area, mean patch size, number of patches, and largest patch size) for each of the four transitional classes were calculated using APACK 2.22 (Mladenoff and DeZonia 2001).

Statistical analyses

We compared vegetation measured at transects and soil properties measured at soil pits among ecotone locations using mixed models (PROC MIXED; SAS 2003). For soil pit analyses, we recognized A, B1, and B2 horizons in which the B1 and B2 horizons were formally classified as Bt(1 or 2), Bk(1 or 2), or Btk(1 or 2) horizons (Soil Survey Staff 1993), depending on the pit. The fixed effect in the vegetation analyses was the variable "side" (grass or sparse), whereas the fixed effect for the soil pit models was "position" (grass, ecotone, sparse, or bare patch). "Transect" (1–4) was treated as a random variable in all mixed-models analyses. Percentage data were arcsine square-root transformed prior to

these analyses. Post hoc comparisons of means were adjusted using the Tukey-Kramer method.

We examined the relationships between soil properties measured at transect points and vegetation variables from the image analysis by spatially joining transect soil data to the transitional classes (ARC/INFO; ESRI 1995). We used logistic regression models (PROC GENMOD; SAS 2003) to relate soil variables to remote-sensed vegetation variables. Explanatory soil variables were (1) surface soil variables (percentage silt at 0–5 cm, percentage clay at 0–5 cm, $CaCO_3$ score at 0–5 cm) and, in separate models, (2) a subsurface soil variable (percentage clay at 10–20 cm). "Side" (grass or sparse) and its interaction with each soil variable were also included. We evaluated three types of models (presently vegetated, vegetation persistence, and vegetation colonization) with different dependent variables. The "presently vegetated" model was the probability that a cell was vegetated in 1996 (127/240 observations for surface soil, 40/70 observations for subsurface clay). The "vegetation persistence" model was the probability that a cell remained vegetated if it was vegetated in 1936 (101/159 observations for surface soil, 34/51 observations for subsurface clay). The "vegetation colonization" model was the probability that a cell became vegetated if it was bare in 1936 (26/81 observations for surface soil, 6/19 observations for subsurface clay). For each model
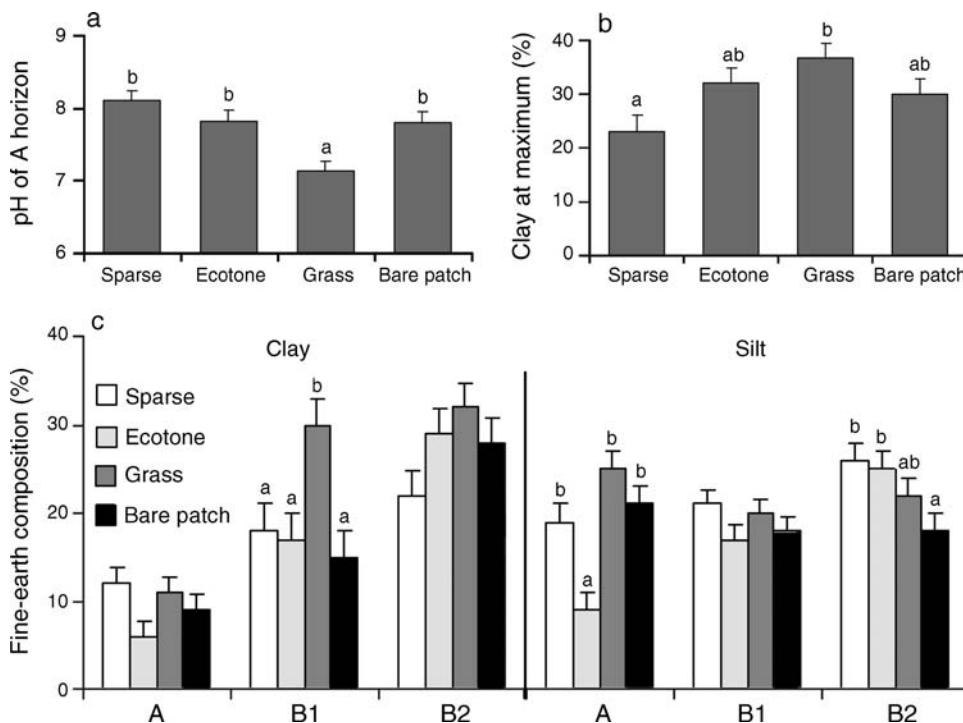
FIG. 3. (a) The pH of the A horizon; (b) the percentage of clay within the soil horizon exhibiting maximum clay content; and (c) the percentage fine-earth composition of silt and clay for each horizon in the soil pits at four pits in each ecotone position. All values are mean + SE. Bars with different lowercase letters were significantly different ($P \leq 0.05$).

involving surface soil variables, we started with a full model including all three variables and sequentially eliminated the least significant variable, and its interaction with "side," if it had $P > 0.10$ and then refit the reduced models. We also examined all possible model subsets. Due to the small sample size, we could not estimate the effect of "side" in the "vegetation colonization" subsurface clay model and computed an exact P value for the "clay" term (EXACT statement; PROC LOGISTIC). Examination of the raw residuals of initial logistic models indicated significant positive autocorrelation at 5–15 m lags in some transects for models with both silt and $CaCO_3$ (PROC ARIMA; SAS 2003). Such autocorrelation may produce significance tests with increased Type I error rates (Legendre 1993). Consequently, we used the method of generalized estimating equations (GEEs) as implemented in PROC GENMOD (SAS 2003; also known as "marginal models") to account for the spatial autocorrelation in the logistic equations (following Albert and McShane 1995). Transects nested within each side of the ecotone were used as subjects (or "clusters"), within-subject locations were specified, and autocorrelation within subjects was modeled as a first-order autoregressive process. A set of common distances within subjects is not required for this approach and GEE estimates of the mean response and SE (with large sample size) are valid even if the within-subject associations are incorrectly specified (Fitzmaurice et al. 2004). The GEE procedure treats

within-subject correlation as a "nuisance variable" to adjust estimates. In our case, there was little difference in parameter means when compared to normal logistic regression. Estimates of parameter standard errors, however, were larger.

RESULTS

Was ecotone position related to soil-geomorphic variation?

We did not find any evidence that a fence line ever existed at the ecotone boundary, but we did find that the ecotone was associated with varying soil properties
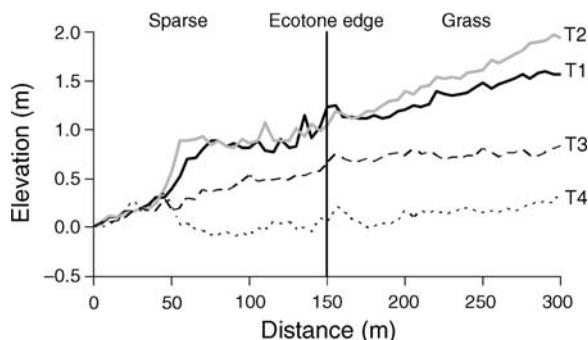

FIG. 4. Microtopographic profiles for each transect (T1–4) at 5-m intervals (estimated error is ±1 cm). All elevation values were standardized with respect to the value at meter 0, which was set at zero.

TABLE 1. Basal cover (mean ± SE) of dominant perennial species along transects on each side of the ecotone ($N = 120$ points/side).

Species	Grass side	Sparse side	P
Grasses			
Pleuraphis mutica	12.3 ± 1.2	1.8 ± 0.59	<0.0001
Muhlenbergia arenacea	0.13 ± 0.05	0.03 ± 0.02	0.067
Scleropogon brevifolius	0.03 ± 0.02	0.05 ± 0.04	0.65
Dasyochloa pulchella	0	0.18 ± 0.04	0.007
Shrubs			
Prosopis glandulosa	0.35 ± 0.14	1.1 ± 0.24	0.052
Lycium berlandieri	0.06 ± 0.04	0.22 ± 0.03	0.24
Flourensia cernua	0.24 ± 0.10	0.009 ± 0.006	0.19

Note: P values indicate significance of differences between sides.

(Figs. 2 and 3). The depth of the A horizons varied among positions across the ecotone ($F = 6.45$, df = 3, 9, $P = 0.013$; Fig. 2a). The contact of the A horizon with the B1 horizon was shallowest in the grass side, deepest at the ecotone, and intermediate on the sparse side. Depth to the B2 contact did not vary across the ecotone. The depth at which the calcium carbonate equivalent values exceeded 1% also varied across the ecotone ($F = 11.73$, df = 3, 9, $P = 0.002$; Fig. 2b). Calcium carbonate content exceeded 1% at the surface on the sparse side, but surface horizons in the ecotone and grass side had low carbonate. Like the sparse side, bare patches in the grass side had high calcium carbonate levels near the surface.

The pH of the A horizon ($F = 8.11$, df = 3, 9, $P = 0.006$; Fig. 3a) and B1 horizon ($F = 10.95$, df = 3, 9, $P = 0.002$; data not shown), were lowest in the grass side, while pH in the B2 horizons did not vary. Electrical conductivity did not vary in any horizon. The maximum percentage clay accumulation observed within the soil profiles was ~13% higher on the grass side than the sparse side; the ecotone and bare patches were intermediate ($F = 3.66$, df = 3, 9, $P = 0.056$; Fig. 3b). The clay content of the B1 horizon was highest on the grass side ($F = 10.8$, df = 3, 9, $P = 0.002$; Fig. 3c). Clay content of the other horizons did not differ. Silt content in the A horizon was lowest at the ecotone ($F = 23.4$, df = 3, 9, $P = 0.0001$). In the B2 horizon, silt was lowest in the large bare patches ($F = 5.85$, df = 3, 9, $P = 0.02$).

Microtopography along the transects indicated that the sparse side generally occupied lower positions in the landscape (by up to 2 m) than the grass side, but this difference diminished with transects 3 and 4, which were located farther upslope (Fig. 4). The microtopography also indicated a localized peak in elevation just to the grass side of the ecotone edge on all four transects, corresponding to the relatively thick A horizon in Fig. 2a. The soil at the peaks was wind-deposited loamy sand.

Was vegetation pattern around the ecotone stable or dynamic?

Current vegetation patterns indicate that *P. mutica* was the dominant plant on both sides of the ecotone, and its basal cover was about seven times higher on the grass side than on the sparse side (Table 1). Conversely, the cover of *P. glandulosa* was about three times higher in the sparse side than the grass side, and *D. pulchella* was also important in the sparse side. The multitemporal image analysis indicated that the ecotone separating these present-day community types has been present since at least 1936. The ecotone moved into the grass side at several places along its length over the subsequent 60 years (Fig. 1). Other parts of the ecotone were stable. Vegetation establishment at the ecotone was rare.

The transitional classes indicated that (1) there were different dynamics on either side of the ecotone, and (2) the dynamics involved stability, vegetation establishment, and vegetation loss occurring in patches (Table 2). Vegetation loss rates were similar on the grass and sparse sides. The grass side, however, experienced a much higher net vegetation loss (the area classified as bare increased from 10% to 30%) than the sparse side (from 50% to 52%). This difference was due to the inability of vegetation establishment to counterbalance vegetation loss on the grass side, whereas establishment was comparable to vegetation loss on the sparse side.

TABLE 2. Landscape metrics for transition classes for the grass side and sparse side of the ecotone.

Transition class	Area (%)	Patch size (m²)	No. patches	Largest patch (m²)
Grass side				
Persistent bare	6.4	13.3 ± 55.5	1439	972
Vegetated to bare	23.5	29.0 ± 84.9	2418	1267
Bare to vegetated	8.3	12.1 ± 26.5	2053	361
Persistent vegetated	61.8	264.2 ± 6634.7	699	175 416
Sparse side				
Persistent bare	29.2	41.4 ± 376.3	2231	11 204
Vegetated to bare	22.6	20.1 ± 101.5	3561	2891
Bare to vegetated	20.9	19.3 ± 95.6	3440	3735
Persistent vegetated	27.3	31.2 ± 476.6	2769	22 150

Notes: The grain of metrics is 1 m², and values are based on an 8-cell neighbor rule. Values for patch size are given as mean ± SD.

TABLE 3. Parameters for the final generalized estimating equation (GEE) models for surface soil properties using a first-order autoregressive correlation structure.

Model	Estimate	SE	Z	P
Presently vegetated				
CaCO₃	−0.54	0.13	−4.12	<0.0001
Side	1.04	0.60	1.72	0.09
CaCO₃ × Side	−0.15	0.27	−0.54	0.59
Vegetation persistence				
CaCO₃	−0.68	0.28	−2.39	0.02
Side	0.83	0.87	0.96	0.34
CaCO₃ × Side	−0.72	0.69	−1.04	0.30
Vegetation colonization				
CaCO₃	−0.50	0.12	−4.17	<0.0001
Side	0.44	0.46	0.94	0.35
CaCO₃ × Side	−0.04	0.24	−0.18	0.85

Notes: The side estimate is positive when side = grass. SE is the empirical standard error estimate.

TABLE 4. The results of logistic regression models for subsurface clay content.

Model	Estimate	SE	χ^2	P
Presently vegetated				
Clay at 10–20 cm	0.18	0.09	8.46	0.0036
Side	2.62	1.95	1.99	0.16
Clay × Side	−0.13	0.09	2.06	0.15
Vegetation persistence				
Clay at 10–20 cm	0.08	0.09	1.26	0.26
Side	0.91	2.29	0.16	0.69
Clay × Side	−0.04	0.11	0.18	0.67
Vegetation colonization				
Clay at 10–20 cm	0.39	0.20	6.25	0.01

Note: The side estimate is positive when side = grass. For the colonization model, there were too few samples to estimate the effect of side.

The average size of patches that exhibited stability or change ranged from 12 to 40 m² except for the stable grass patches of the grass side, in which a single patch accounted for 59% of the grass side (Table 2). Dynamic patches tended to involve many small patches rather than a few large contiguous areas.
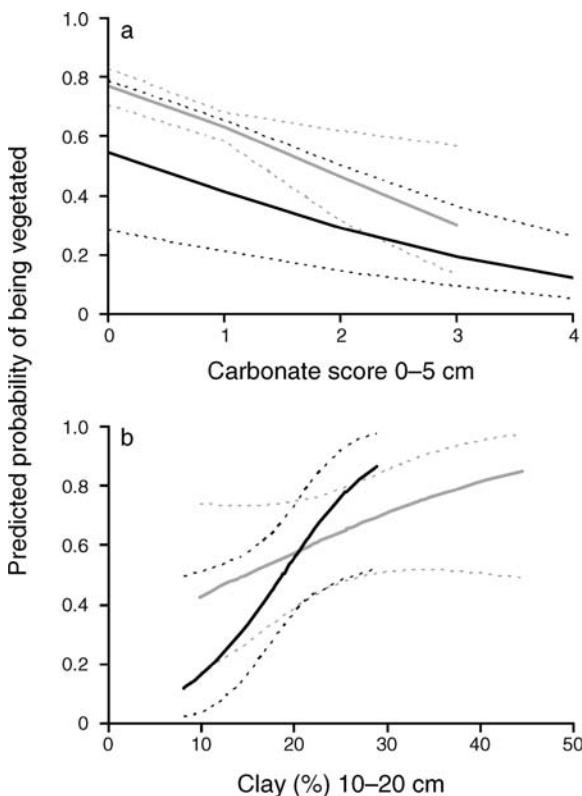

FIG. 5. Predicted probabilities (solid line) that a cell was vegetated in 1996 from (a) the generalized estimating equation model for surface soil and (b) the logistic regression model for subsurface clay. Dotted lines indicate 95% CI. Estimates are shown for each side of the ecotone (black, sparse side; gray, grass side).

Were vegetation changes around the ecotone related to soil properties?

Variation in soil properties was clearly related to vegetation pattern and dynamics within each side of the ecotone. Of the surface soil variables, only surface CaCO₃ was retained in the presently vegetated, vegetation persistence, and vegetation colonization models (Table 3). The strong negative effect of CaCO₃ on the vegetation variables was similar within each side of the ecotone (Fig. 5a; vegetation persistence and colonization patterns were similar to those in Fig. 5a). When considered alone, surface silt was positively related to vegetation presence in 1996 and vegetation persistence, but not colonization (data not shown). Surface clay was not significant when considered alone. Subsurface clay, on the other hand, was positively related to vegetation presence (in a similar way on both sides of the ecotone; Fig. 5b) and colonization (Table 4). The exact test for the colonization model ($P = 0.02$) also indicated that the parameter estimate was significantly different from zero.

DISCUSSION

Was ecotone position related to soil-geomorphic variation?

Although the soils on either side of the ecotone could be informally grouped as "sandy loams" based on surface textures, the two sides of the ecotone exhibited significant differences in soil properties. The sparse side occupied a slightly lower landscape position on soils with higher surface carbonate and a less well developed argillic horizon compared with the grass side. The more strongly developed and elevated soils of the grass side probably represent a remnant surface, whereas the sparse side represents an exhumed surface exposing calcareous material. Erosion from the generally bare side has accentuated microtopographic differences across the ecotone as coarse sediments are transferred by wind to the grass-dominated side. Finally, the unique soils in the large bare areas within the grass side suggest that the argillic horizons in some of these patches have

been obliterated (sensu Gile 1975) and carbonate has been redistributed to the surface via bioturbation by mound-building kangaroo rats (*Dipodomys spectabilis*).

These analyses clearly indicate that geomorphic processes have produced ecologically significant soil variation related to (and reinforcing) ecotone position as well as large patches around it. It is notable that this significant variation did not involve large or obvious contrasts between "sandy" or "clayey" soils (e.g., HilleRisLambers et al. 2001).

Was vegetation pattern around the ecotone stable or dynamic?

The pattern of vegetation change did not indicate vegetation stability or directional movement of the ecotone (e.g., Risser 1995), but a fine-scale shifting mosaic or patch-dynamic system (Aguiar and Sala 1999) surrounding an ecotone. Although vegetation loss occurred at several areas along the ecotone boundary, much of the boundary was stable and most vegetation change occurred in patches across the study area. Furthermore, vegetation loss was balanced to varying degrees by vegetation establishment within each side of the ecotone. These dynamics suggest that the position of the ecotone is not solely governed by changes at the ecotone boundary (i.e., a switch ecotone; Wilson and Agnew 1992), but ecotone position may be determined largely by differential patch dynamics occurring across a broader area.

The two sides of the ecotone can be regarded as alternative states distinguished by different proportions, sizes, and dynamics of vegetated and bare patches. The sparse side was essentially stable at a broad scale over the 60-year period, with vegetation loss occurring in mostly small (20-m^2) patches balanced by vegetation establishment in a similar number and size of patches. The observation that similar soils in other parts of the Chihuahuan Desert maintain grasslands, as well as the presence of remnant *P. mutica* and *Muhlenbergia porteri* Scribn. ex Beal. grass plants in bare areas, suggests that the sparse side supported a more continuous grassland in the past. Thus, we suggest that the sparse side has undergone a persistent transition from grass-dominated to a sparsely vegetated state. The elevated rates of net vegetation loss on the grass side suggest that it may be undergoing a transition, but it is impossible to say with certainty.

The broadscale stability of the sparsely vegetated side over 60 years, however, counters the expectation that such fragmented landscapes should show accelerating degradation of vegetation (e.g., Davenport et al. 1998). Based on mathematical modeling, van de Koppel and Rietkerk (2004) suggested that spatial transfers of water may buffer vegetation degradation under conditions that would otherwise lead to vegetation collapse in nonspatial models. The dynamic nature of fine-scale vegetated patches may indicate the consequences of such spatial transfers and their role in maintaining broader

scale stability. It is possible that erosion and sedimentation patterns that alter the source and destination of spatial transfers of water over time (Puigdefábregas 2005) could give rise to the dynamics we observed.

Were vegetation changes around the ecotone related to soil properties?

Variation in soil properties was clearly related to the patchy vegetation cover as well as historical changes in vegetation within each part of the ecotone. Surface $CaCO_3$ and subsurface clay were strong predictors of vegetation presence and colonization patterns, and $CaCO_3$ additionally predicted the persistence of vegetation. The soil variation, however, may involve an effect of recent vegetation presence or absence that is related to erosion processes (e.g., Neff et al. 2005), as well as variation caused by long-term geomorphic evolution (Gile and Grossman 1997). Thus, soil properties are simultaneously a cause and effect of vegetation processes. General notions suggest that these soil components have strong effects on water infiltration and retention (McAuliffe 1994, Gile and Grossman 1997) that may influence plant survival and establishment. The precise mechanisms by which $CaCO_3$ and clay may mediate the fine scale of resistance and resilience of vegetation (especially *P. mutica*), however, are not yet clear.

An integrated view of vegetation dynamics

Our results suggest that theoretical development to explain the existence and patterning of alternative states in semiarid vegetation should better account for soil-geomorphic properties. Subtle variations in multiple soil attributes clearly affect ecosystem resilience (Maestre et al. 2003), and high spatial heterogeneity in attribute values is a characteristic of many real arid systems (e.g., Stafford Smith and Morton 1990, Maestre and Cortina 2002, McAuliffe 2003). More generally, spatial and temporal variation in adaptive capacity (sensu Gunderson 2000) is a common property of complex systems that describes the ability of a system to remain within a stability domain (e.g., grassland) under disturbance. A key issue, then, is to define the attributes, their value ranges, and the spatial scales over which values vary to produce significant differences in adaptive capacity. Our results indicate that subtle differences in particular soil attributes may help to explain transitions in arid ecosystems: a few decimeters' difference in elevation, slight differences in clay content, and deep vs. disseminated calcium carbonate distinguished patches that were vulnerable to vegetation loss (and colonization) from those that were resistant to them. These patches were usually a few tens of square meters in area. Their pattern of aggregation, in turn, may determine broader scale resilience and the presence of the ecotone.

The strong relationship between vegetation dynamics and soil properties that we observed does not support a pure self-organization model (HilleRisLambers 2001),

but the strong dynamics suggest that soils alone cannot explain vegetation pattern. Soil heterogeneity clearly affected the evolution of vegetation pattern (see Malanson et al. [2002] for another view). Our results raise the possibility that only a subset of soil patches within a landscape is susceptible to transitions over a given period. Thus, self-organizing processes occur, but their spatial expression at multiple scales (e.g., as an ecotone, bands, or patches) can be constrained by a slow-changing template of soil variation and feedback to particular soil attributes (Pringle and Tinley 2003). This "ecogeomorphic" view of vegetation patterning (Monger et al. 1998) focuses on the interactions between ecological (e.g., grazing effects on plants and spatial interactions) and geomorphic (e.g., soil change) processes, and blends previously contrasting explanations based either on underlying soil heterogeneity or vegetation–resource feedbacks (e.g., Tongway et al. 2001).

Literature Cited

Aguiar, M. R., and O. E. Sala. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. Trends in Ecology and Evolution 14:273–277.

Albert, P. S., and L. M. McShane. 1995. A generalized estimating equations approach for spatially correlated binary data: applications to the analysis of neuroimaging data. Biometrics 51:627–638.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience 2:83–99.

Archer, S., C. Scifres, C. R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs 52: 111–127.

Bestelmeyer, B. T., J. E. Herrick, J. R. Brown, D. A. Trujillo, and K. M. Havstad. 2004. Land management in the American Southwest: a state-and-transition approach to ecosystem complexity. Environmental Management 34:38–51.

Blom, R. G., and M. Daily. 1982. Radar image processing for rock-type discrimination. Institute of Electrical and Electronics Engineers, Inc. (IEEE) Transactions on Geoscience and Remote Sensing 20:343–351.

Brady, N. C., and R. R. Weil. 2002. The nature and properties of soils, Thirteenth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen. 1998. Viewpoint: sustainability of piñon-juniper ecosystems—a unifying perspective of soil erosion thresholds. Journal of Range Management 51:231–240.

d'Herbes, J-M., C. Valentin, D. J. Tongway, and J-C. Leprun. 2001. Banded vegetation patterns and related structures. Pages 1–19 *in* D. J. Tongway, C. Valentin, and J. Seghieri, editors. Banded vegetation patterning in arid and semiarid environments: ecological processes and consequences for management. Ecological Studies 149. Springer-Verlag, New York, New York, USA.

Dunkerley, D. L., and K. J. Brown. 2002. Oblique vegetation banding in the Australian arid zone: implications for theories of pattern evolution and maintenance. Journal of Arid Environments 51:163–181.

ERDAS. 1999. IMAGINE software and on-line help manual. Leica Geosystems, Atlanta, Georgia, USA.

ESRI. 1995. ARC/INFO software. Environmental Systems Research Institute, Redlands, California, USA.

Fitzmaurice, G. M., N. M. Laird, and J. H. Ware. 2004. Applied longitudinal analysis. John Wiley and Sons, Hoboken, New Jersey, USA.

Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. Journal of Range Management 44:422–426.

Gee, G. W., and J. W. Bauder. 1986. Particle-size analysis. Pages 383–411 *in* A. Klute, editor. Methods of soil analysis, part 1. Physical and minerological methods, Second Edition. American Society of Agronomy, Madison, Wisconsin, USA.

Gibbens, R. P., R. P. McNeely, K. M. Havstad, R. F. Beck, and B. Nolen. 2005. Vegetation changes in the Jornada Basin from 1858 to 1998. Journal of Arid Environments 61:651–668.

Gile, L. H. 1961. A classification of Ca horizons in soils of a desert region, Dona Ana County, New Mexico. Soil Science Society of America Proceedings 25:52–61.

Gile, L. H. 1975. Causes of soil boundaries in an arid region; II. dissection, moisture, and faunal activity. Soil Science Society of America Proceedings 39:324–330.

Gile, L. H., and R. B. Grossman. 1997. The desert project soil monograph. Natural Resources Conservation Service, USDA National Soil Survey Center, Lincoln, Nebraska, USA.

Graetz, R. D., and D. J. Tongway. 1986. Influence of grazing management on vegetation, soil structure, and nutrient distribution and the infiltration of applied rainfall in a semi-arid chenopod shrubland. Australian Journal of Ecology 11:347–360.

Grossman, R. B., D. S. Harms, C. A. Seybold, L. A. Pytlik, and J. E. Herrick. 2001. Coupling use-dependent and use-invariant data for soil quality evaluation. Journal of Soil and Water Conservation 56:63–68.

Gunderson, L. H. 2000. Ecological resilience—in theory and application. Annual Review of Ecology and Systematics 31: 425–439.

Hamerlynck, E. P., J. R. McAuliffe, and S. D. Smith. 2000. Effects of surface and sub-surface soil horizons on the seasonal performance of *Larrea tridentata* (creosotebush). Functional Ecology 14:596–606.

Hennessy, J. T., R. P. Gibbens, J. M. Tromble, and M. Cardenas. 1983. Water properties of caliche. Journal of Range Management 36:723–726.

HilleRisLambers, R., M. Rietkerk, F. van den Bosch, H. H. T. Prins, and H. de Kroon. 2001. Vegetation pattern formation in semi-arid grazing systems. Ecology 82:50–61.

Lajtha, K., and W. H. Schlesinger. 1988. The effect of $CaCO_3$ on the uptake of phosphorus by two desert shrub species, *Larrea tridentata* (DC.) Cov. and *Parthenium incanum* H. B. K. Botanical Gazette 149:328–334.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

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

Ludwig, J. A., and D. J. Tongway. 1997. A landscape approach to rangeland ecology. Pages 1–12 *in* J. Ludwig, D. Tongway, D. Freudenberger, J. Noble, and K. Hodgkinson, editors. Landscape ecology, function and management: principles

from Australia's rangelands. CSIRO Publishing, Colling-wood, Victoria, Australia.

Ludwig, J. A., B. P. Wilcox, D. D. Breshears, D. J. Tongway, and A. C. Imeson. 2005. Vegetation patches and runoff-erosion as interacting eco-hydrological processes in semiarid landscapes. Ecology **86**:288–297.

Maestre, F. T., and J. Cortina. 2002. Spatial patterns of surface properties and vegetation in a Mediterranean semi-arid steppe. Plant and Soil **241**:279–291.

Maestre, F. T., J. Cortina, S. Bautista, J. Bellot, and R. Vallejo. 2003. Small-scale environmental heterogeneity and spatio-temporal dynamics of seedling establishment in a semiarid degraded ecosystem. Ecosystems **6**:630–643.

Malanson, G. P., D. R. Butler, D. M. Cairns, T. E. Welsh, and L. M. Resler. 2002. Variability in an edaphic indicator in alpine tundra. Catena **49**:203–215.

Mauchamp, A., C. Montaña, J. Lepart, and S. Rambal. 1993. Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. Oikos **68**:107–116.

McAuliffe, J. R. 1994. Landscape evolution, soil formation, and ecological patterns and processes in Sonoran desert bajadas. Ecological Monographs **64**:111–148.

McAuliffe, J. R. 2003. The interface between precipitation and vegetation: the importance of soils in arid and semiarid environments. Pages 9–27 *in* J. F. Weltzin and G. R. McPherson, editors. Changing precipitation regimes and terrestrial ecosystems. University of Arizona Press, Tucson, Arizona, USA.

Mladenoff, D. J., and B. DeZonia. 2001. APACK analysis software and user's guide. University of Wisconsin, Madison, Wisconsin, USA.

Monger, H. C., D. R. Cole, J. W. Gish, and T. H. Giordano. 1998. Stable carbon and oxygen isotopes in Quaternary soil carbonates as indicators of ecogeomorphic changes in the northern Chihuahuan Desert, USA. Geoderma **82**:137–172.

Neff, J. C., R. L. Reynolds, J. Belnap, and P. Lamothe. 2005. Multi-decadal impacts of grazing on soil physical and biogeochemical properties in southeast Utah. Ecological Applications **15**:87–95.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics **4**: 25–51.

Peters, D. P. C. 2002. Plant species dominance at a grassland-shrubland ecotone: an individual-based gap dynamics model or herbaceous and woody species. Ecological Modeling **152**: 5–32.

Pringle, H., and K. Tinley. 2003. Are we overlooking critical geomorphic determinants of landscape change in Australian rangelands? Ecological Management and Restoration **4**:180–186.

Puigdefábregas, J. 2005. The role of vegetation patterns in structuring runoff and sediment fluxes in drylands. Earth Surface Processes and Landforms **30**:133–147.

Reynolds, J. F., P. R. Kemp, K. Ogle, and R. J. Fernández. 2004. Modifying the pulse–reserve paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. Oecologia **141**:194–210.

Reynolds, J. F., and D. M. Stafford Smith. 2002. Global desertification: Do humans cause deserts? Dahlem Workshop Report 88, Dahlem University Press, Berlin, Germany.

Rietkerk, M., S. C. Dekker, P.C. de Ruiter, and J. van de Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science **305**:1926–1929.

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

SAS Institute. 2003. SAS 9.1.3 Help and documentation. SAS Institute, Cary, North Carolina, USA.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Scull, P., J. Franklin, O. A. Chadwick, and D. McArthur. 2003. Predictive soil mapping: a review. Progress in Physical Geography **27**:171–197.

Soil Survey Staff. 1993. Soil survey manual. USDA Agriculture Handbook 18. USDA Natural Resources Conservation Service, National Soil Survey Center, Lincoln, Nebraska. USA.

Stafford Smith, D. M., and S. R. Morton. 1990. A framework for the ecology of arid Australia. Journal of Arid Environments **18**:255–278.

Tongway, D. J., C. Valentin, , and J. Seghieri, editors. 2001. Banded vegetation patterning in arid and semiarid environments: ecological processes and consequences for management. Ecological Studies 149. Springer-Verlag, New York, New York, USA.

van de Koppel, J., and M. Rietkerk. 2004. Spatial interactions and resilience in arid ecosystems. American Naturalist **163**: 113–121.

Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedbacks switches in plant communities. Advances in Ecological Research **23**:263–336.

APPENDIX

Photograph of the Corralitos ecotone. (*Ecological Archives* E087-056-A1).