

Distribution of plant species at a biome transition zone in New Mexico

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Abstract.

Question: Is there a difference in plant species and life form composition between two major patch types at a biome transition zone? Are subordinate species associated with different patch types at the shortgrass steppe - Chihuahuan desert grassland transition zone? Is this association related to differences in soil texture between patch types and the geographic range of associated species?

Location: central New Mexico, USA.

Methods: Patches dominated by either *Bouteloua gracilis*, the dominant species in the shortgrass steppe, or *Bouteloua eriopoda*, dominant species in the Chihuahuan desert grasslands, were sampled for the occurrence of subordinate species and soil texture within a 1500-ha transitional mosaic of patches.

Results: Of the 52 subordinate species analysed, 16 species were associated with *B. gracilis*-dominated patches and 12 species with *B. eriopoda*-dominated patches. Patches dominated by *B. gracilis* were richer in annual grasses and forbs, whereas patches dominated by *B. eriopoda* contained more perennials forbs and shrubs. Soils of *B. gracilis*-dominated patches had higher clay and lower rock contents compared with soils of *B. eriopoda*-dominated patches. Differences in species characteristics of the dominant species as well as differences in soil texture between patch types contribute to patch-scale variation in composition. The association of species to patch types was not related to their geographic range and occurrence in the adjacent biomes.

Conclusions: Patch types at this biome transition zone have characteristic life-form and species composition, but species are associated to patch types due to local constraints, independently from their affinity to the adjacent biomes.

Keywords: Association; *Bouteloua gracilis*; *Bouteloua eriopoda*; Chihuahuan desert grassland; Geographic range; Life form; Patch mosaic; Semi-arid grassland; Short-grass steppe; Soil texture; Species composition.

Nomenclature: Anon. (1999).

Abbreviation: SNWR = Sevilleta National Wildlife Refuge.

Introduction

The geographic location of biome transition zones is primarily determined by climatic factors, thus fluctuations or directional changes in climate are expected to have large effects on these areas, such as shift in species dominance and change in species composition (di Castri et al. 1988; Risser 1995). Broad-scale transitions between biomes usually consist of a mosaic of patches of different types that are characterized by the dominance or codominance by species from one or more of the two adjacent biomes (Gosz 1993; Gosz & Gosz 1996). Most studies on biome transition zones focus on these dominant species (Lavoie & Payette 1996; Barras & Kellman 1998; Minnick & Coffin 1999; Weltzin & McPherson 1999; Anand & Li 2001) or life forms ('phase transitions'; Timoney et al. 1993; Loehle et al. 1996). By contrast, patterns in species and life form composition are not well documented and understood in these transitional areas, although it is these species that determine patterns in biodiversity.

The most common approach to studying biome transition zones is along transects between the adjacent biomes and through the transition between them. These transects reveal changes in a single or few variables across biome transition zones, and usually address patch structure (Timoney et al. 1993) or the performance of the dominant species (Lavoie & Payette 1996; Minnick & Coffin 1999). A different approach is to focus on one, usually intermediate area along this broad-scale transect and study patch types in more detail within this area. This approach is more applicable when conducting experiments (Wesser & Armbruster 1991; Weltzin & McPherson 1999), studying fine-scale patterns of environmental variables (Barras & Kellman 1998), analyzing changes in patch structure through time (Loehle et al. 1996), and also when patterns in species composition are addressed (Hovestadt et al. 1999).

Patch types within biome transition zones have been conceptualized as representatives of the two adjacent

biomes based on the dominant species (Gosz 1993; Risser 1995). While adjacent biomes differ in species and life form composition (Cox & Moore 1985; Begon et al. 1996), it is unclear if patch types at the transition zone also differ in these features. Since the dominant species of these patch types dominate at different geographic areas in the broad scale (biomes), we hypothesize that they occupy and provide different habitats for the subordinate species at the landscape scale of the biome transition zone. Subordinate species may be associated with these patch types due to differences between the dominant species (growth form, competitive ability, etc.), but also due to potential environmental differences between patch types (topography, soil characteristics, disturbance regime, etc.). Subordinate species occurring at a biome transition zone may have very different geographic ranges that include the two adjacent biomes (Neilson et al. 1992; Risser 1995). Thus, it is a further question if species found associated with the two patch types at the transition zone differ in their geographic range and occurrence in the adjacent biomes.

In central New Mexico, a broad-scale transition zone occurs between the short-grass steppe dominated by *Bouteloua gracilis* and the Chihuahuan desert grassland dominated by *B. eriopoda* (Gosz 1993). Although shortgrass steppe and Chihuahuan desert grassland vegetation types are dominated by congeneric species, they represent different biomes, temperate grassland and desert (Cox & Moore 1985), respectively. Each biome occupies geographically and climatically distinct areas that also differ in species composition, disturbance regime, and evolutionary history of grazing by large herbivores (Lauenroth & Milchunas 1992; Schmutz et al. 1992; Sims & Risser 2000; Hochstrasser et al. 2002). Landscapes within this transition zone contain a mosaic of patches dominated by one or both *Bouteloua* species (Gosz & Gosz 1996).

Several studies have examined patterns in, and controls on, species dominance and structure of this biome transition zone (Gosz 1993; Gosz & Gosz 1996; Fields et al. 1999; Minnick & Coffin 1999; Peters 2000; Anand & Li 2001). However, patterns in species composition relative to patch types of the two *Bouteloua* species have not been addressed. Since in semi-arid climates the most important limiting factor is soil water availability (Noy-Meir 1973), we hypothesized that this factor may affect fine-scale species distribution patterns within the biome transition zone. Therefore, our study of subordinate species composition was accompanied with a survey of soil texture, the most important determinant of soil water availability in semiarid regions (Noy-Meir 1973; Sala et al. 1988; Buxbaum 1997).

The overall objective of this study was to assess the species composition of patch types dominated either by

B. gracilis or *B. eriopoda* at a shortgrass steppe – Chihuahuan desert grassland transition zone. Specific objectives were: (1) to test if subordinate species are associated with patch types dominated either by *B. gracilis* or *B. eriopoda*, (2) to compare the life form composition of the two patch types, (3) to compare the soil texture between the two patch types and test its relationship with life form composition, and (4) to examine if the association of species to patch types at the transition zone is related to their geographic range and occurrence in the adjacent biomes.

Methods

Site description

The study area is the Sevilleta National Wildlife Refuge (SNWR; 34.5°N, 106.9°W) located in central New Mexico, USA. Grazing by cattle has been excluded from the SNWR since 1973, although grazing by native herbivores, such as pronghorn antelope and rabbits, occurs at low to moderate intensities. The climate of the area is subtropical semiarid. Mean monthly temperatures recorded in Socorro, south of the SNWR at similar elevation and topography, range from 2.6°C in January to 24.6°C in July. Long-term (65yr) mean annual precipitation is 232 mm (SD = 79) (Peters 2000). Local, but intense summer thunderstorms between 1 July and 1 November account for 60% of the annual precipitation. A complete site description is available from <http://sevilleta.unm.edu>.

The study site was the McKenzie Flats (1650 m elevation) where vegetation is typical of the shortgrass steppe - Chihuahuan desert grassland transition zone. Patches of vegetation of variable size (< 10 m² to > 1000 m²) and shape may be dominated or co-dominated by *B. gracilis* and *B. eriopoda* at this location. The topography is level on sandy loam or loamy sand soils with > 64% sand content.

Patch selection

Aerial photos from 1993 were used to identify patches potentially dominated by either *B. gracilis* or *B. eriopoda* based upon color contrast and field experience. Several criteria were then used in the field to select a patch for sampling: plant cover dominated by one of the two *Bouteloua* species (> 90% of total vegetation cover), a minimum diameter (20 m) to allow multi-scale sampling, the lack of active or abandoned kangaroo rat mounds or other soil disturbance within the patch, and a distance of more than 300 m from another patch of the same type to minimize problems of spatial autocorrelation.

No neighbouring patches of a single type were selected to ensure the interspersion of patch types and to avoid pseudo-replication (Hurlbert 1984).

For each patch type 30 patches were randomly selected from the patches available that fit our criteria, totalling 60 sampling sites. Due to the low frequency of mono-dominant patches and the rigorous criteria of site selection, sample patches were spread over a 1500-ha area.

Vegetation and soil sampling

Starting from the center of each patch, we sampled the vegetation for presence/absence of species in a series of nested circular plots of increasing diameter in August 1997, the peak of the growing season. By doubling the size of the sample plot in each of ten increments, plot size ranged from 0.25 m² to 256 m². The upper limit for plot size was constrained by patch size. A series of plot sizes was used since species associations may be dependent on plot size (Greig-Smith 1985). At a particular plot size, rare species may have too low frequencies, whereas abundant species may have too high frequencies (occurring in all plots) for a statistical analysis of associations. Thus, the application of multiple plot sizes may increase the number of species associations detected.

In each patch, three 5 cm-diameter soil samples were randomly collected to a depth of 20 cm. Samples were mixed within each patch and sieved to remove coarse particles (> 2 mm, rocks) that were weighed and expressed as the percentage of the total soil sample weight. The fine fraction was then analyzed for percentage clay, silt, and sand content using the hydrometer method (Day 1965).

Species associations and life form composition

The association of subordinate species to patch type was tested using χ^2 test with a Yates correction (Zar 1999). Our definition of subordinate species covers all vascular plant species found except the two dominants. For each plot size, we tested the association between each species and patch type separately. A species was accepted as being associated with a patch type if a significant association was found for at least one plot size. Species with less than six occurrences (out of 60) at a given plot size were not tested at that size since they cannot be associated statistically with a patch type.

Species were also classified based on their life form: perennial forbs, perennial grasses, annual forbs, annual grasses, shrubs and sub-shrubs, and succulents. In some of the analyses we combined the functionally similar groups, such as the annual forbs and annual grasses into annuals, and the perennial forbs and shrubs into deep-

rooted perennials. We compared overall species richness and species richness by life form between patch types for each plot size. We applied the non-parametric Mann-Whitney *U*-test to compare patch types because values for some life forms and plot sizes had skewed distributions (Zar 1999). For similar reasons, we used Mann-Whitney *U*-test to compare % rock, sand, silt, and clay content of soils from the two patch types. Statistical analyses were performed with Statistica for Windows program package (Anon. 1996) with a level of significance of 0.05.

In addition to comparing the two patch types with respect to soil texture and life form composition, we were also interested in the relationship between soil texture and life form composition. In order to exclude the effect of patch type, we did this analysis separately for *B. gracilis*- and *B. eriopoda*-dominated patches ($n = 30$). We applied Spearman rank correlation to test for correlation between texture class (e.g. % clay) and life form (e.g., number of perennial forbs) (Zar 1999).

Characterizing the geographic distribution of species

Only species significantly associated with one or the other patch type at the biome transition zone were selected for the geographic analysis. Three approaches were used to characterize the geographic distribution of each associated species relative to the shortgrass steppe and the Chihuahuan desert grassland. Because no detailed distribution maps are available for vascular plant species of North America, we first used floristic manuals (Kearney & Peebles 1964; Corell & Johnston 1970; The Great Plains Flora Association 1986) and an on-line database (Anon. 1999) to obtain an overview of the broad-scale distribution of species.

In our second approach, we used an atlas of county-based distribution of all vascular plant species within the Great Plains, which includes the shortgrass steppe, but not the Chihuahuan Desert (Anon. 1977). After delineating the shortgrass steppe within the Great Plains based on Lauenroth & Milchunas (1992), we counted for each species the number of counties in the shortgrass steppe where the species occurred (out of 78 counties). As another measure of distribution, we used the latitude of the northernmost occurrence of each species within the shortgrass steppe and the Great Plains, because shortgrass steppe represents the northern biome at the transition zone. Species not extending into the Great Plains or extending beyond the northern boundary of the map were given the minimum or maximum latitude value, respectively. We applied Mann-Whitney *U*-test to compare the two species groups in terms of the number of counties with occurrences in the shortgrass steppe and the latitude of northernmost occurrence (Zar 1999).

Since no detailed county distribution maps were available for the Chihuahuan Desert, we could not make a similar analysis for species distributions in this biome. In a simple analysis (third approach), however, we looked at what proportion of the species that were associated to one or the other patch type at the transition zone occurred in a typical Chihuahuan Desert site, the Jornada Experimental Range, southern New Mexico. We used a species list from an intensive study we conducted in 50 ha of *B. eriopoda*-dominated grassland in 1996 (see Hochstrasser et al. 2002 for the species list).

Results

Species associations with patch type

A total of 87 subordinate species were found in the 60 patches that included 4 annual grasses, 23 annual forbs, 10 perennial grasses, 38 perennial forbs, 8 shrubs and subshrubs, and 4 succulents. Most annuals and perennial grasses are C4, whereas most perennial forbs and shrubs are C3 species. At the largest plot size, 52 species occurred in at least six patches; these species were analyzed for association with patch type (Table 1). 28 of these 52 species were associated with one of the two patch types for at least one plot size. 16 species were associated with patches dominated by *B. gracilis*, and 12 with patches dominated by *B. eriopoda*. Most species associated with *B. gracilis* were annual forbs (8) whereas most species associated with *B. eriopoda* were perennial forbs (7). Most species showed significant association along a range of plot sizes.

Life form composition and soil texture

For each plot size, the total number of species was similar in the two patch types: at the largest plot size it was on average 25.4 (SD = 6.1) for *B. gracilis*-dominated patches and 23.5 (SD = 3.4) for *B. eriopoda*-dominated patches. Results for life form composition based on all 87 subordinate species were similar for all plot sizes, thus only results for an intermediate size (128 m²) are shown (Fig. 1). *B. gracilis*-dominated patches had a greater number of annual forb and annual grass species, whereas *B. eriopoda*-dominated patches were richer in perennial forbs, and shrubs and subshrubs. The numbers of perennial grasses and succulents per plot were similar in the two patch types.

For soils, the percentage of rock fraction in the 0-20 cm depth was smaller and the percentage of clay fraction was larger in patches dominated by *B. gracilis* compared to patches dominated by *B. eriopoda*, although values overlapped considerably (Fig. 2). Silt and

Table 1. The association of subordinate species to patch type. Species with at least six occurrences are listed. For species that were associated in a range of plot sizes, the sizes of smallest and largest plots are given. N.A. = data not available; * marks species that were left out of the geographic analysis because of their unknown geographic range; Spec. 1 = unidentified species).

Species	Photo-synthetic pathway	Overall frequency at the largest plot size (out of 60)	Plot size (m ²) at which significant association was found	
			<i>B. eriopoda</i> type	<i>B. gracilis</i> type
Annual grasses				
<i>Aristida adscensionis</i>	C ₄	13	-	256
<i>Bouteloua barbata</i>	C ₄	30	-	2 and 8
<i>Monroa squarrosa</i>	C ₄	8	-	-
Annual forbs				
<i>Astragalus nuttallianus</i>	C ₃	8	-	-
<i>Chamaesyce revoluta</i>	C ₄	9	-	-
<i>Chamaesyce serpyllifolia</i>	C ₄	31	-	0.25-256
<i>Chamaesyce serrula</i>	C ₄	27	-	4-256
<i>Euphorbia dentata</i>	C ₄	14	-	128-256
<i>Ipomoea costellata</i>	C ₃	15	-	64-256
<i>Kallstroemia parviflora</i>	C ₄	17	-	128-256
<i>Linum</i> spec.*	N.A.	16	64-256	-
<i>Mollugo cerviana</i>	C ₄	8	-	8
<i>Pectis angustifolia</i>	C ₄	42	-	0.25-256
<i>Salsola tragus</i>	C ₄	45	8-32	-
<i>Sanvitalia abertii</i>	N.A.	6	-	256
<i>Tidestromia lanuginosa</i>	C ₄	18	-	-
Perennial grasses				
<i>Aristida purpurea</i>	C ₄	26	64-256	-
<i>Dasyochloa pulchella</i>	C ₄	43	-	-
<i>Muhlenbergia torreyi</i>	C ₄	32	-	-
<i>Pleuraphis jamesii</i>	C ₄	37	-	2-256
<i>Scleropogon brevifolius</i>	C ₄	22	-	64-256
<i>Sporobolus flexuosus</i>	C ₄	60	0.25	-
Perennial forbs				
<i>Allionia incarnata</i>	C ₄	12	-	-
<i>Aphanostephus ramosissimus</i>	C ₃	7	64-256	-
<i>Astragalus missouriensis</i>	N.A.	21	-	-
<i>Astragalus tephrodes</i>	C ₃	22	128-256	-
<i>Baileya multiradiata</i>	C ₃	7	-	-
<i>Caesalpinia drepanocarpa</i>	C ₃	47	2-256	-
<i>Caesalpinia jamesii</i>	C ₃	15	128-256	-
<i>Chaetopappa ericoides</i>	C ₃	37	-	-
<i>Chamaesyce albomarginata</i>	C ₄	18	-	16-256
<i>Chamaesyce fendleri</i>	C ₄	12	-	-
<i>Dalea nana</i>	C ₃	18	-	-
<i>Evolvulus nuttallianus</i>	C ₃	15	-	-
<i>Gaillardia pinnatifida</i>	C ₄	22	-	-
<i>Glandularia wrightii</i> *	C ₃	10	-	128-256
<i>Hymenopappus filifolius</i>	C ₄	32	-	-
<i>Machaeranthera pinnatifida</i>	C ₃	43	2-256	-
<i>Psilostrophe tagetina</i>	C ₃	25	16-256	-
<i>Solanum elaeagnifolium</i>	C ₃	43	-	16-32; 256
Spec. 1.	N.A.	7	-	-
<i>Sphaeralcea hastulata</i>	C ₃	48	-	16-128
<i>Sphaeralcea wrightii</i>	C ₃	56	4-64	-
<i>Stephanomeria pauciflora</i>	C ₃	10	-	-
Shrubs and subshrubs				
<i>Ephedra torreyana</i>	C ₃	43	-	-
<i>Yucca glauca</i>	C ₃	32	-	-
<i>Gutierrezia sarothrae</i>	C ₃	49	16-256	-
<i>Senecio flaccidus</i>				
<i>Zinnia grandiflora</i>				
Succulents				
<i>Mamillaria</i> spec.	CAM	11	-	-
<i>Opuntia imbricata</i>	CAM	14	-	-
<i>Opuntia phaeacantha</i>	CAM	40	-	-

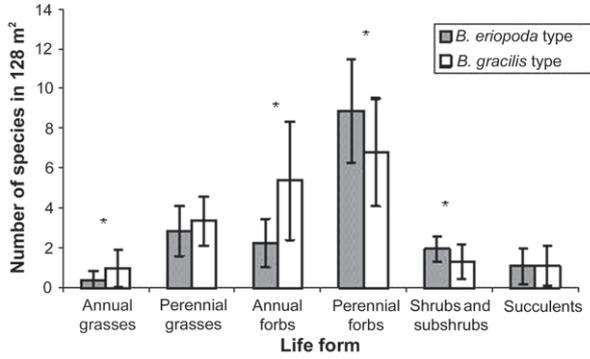


Fig. 1. Life form composition in *B. eriopoda*- and *B. gracilis*-dominated patches in the 128-m² plots (average ± SD). * indicates significant difference between patch types and within life form.

sand content were similar in the two patch types.

To test for the correlation between texture and life form by patch type, we used clay content and the combined life forms of annuals (annual grasses + annual forbs) and deep-rooting perennials (perennial forbs + shrubs and subshrubs), since the functionally similar life forms responded similarly to patch types (Fig. 1). The number of annual species was positively correlated with clay content in patches dominated by *B. gracilis* (Spearman's $R = 0.39, p < 0.05$), and was not correlated significantly in patches dominated by *B. eriopoda* (Spearman's $R = -0.35$, not significant). The number of deep-rooting perennials was negatively correlated with clay content in patches dominated either by *B. gracilis* (Spearman's $R = -0.38, p < 0.05$) or by *B. eriopoda* (Spearman's $R = -0.39, p < 0.05$).

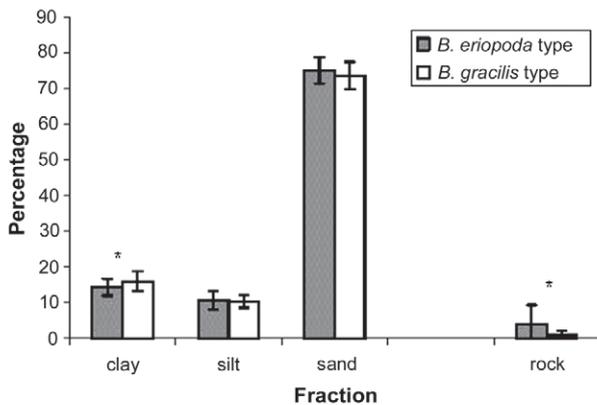


Fig. 2. Soil texture in *B. eriopoda*- and *B. gracilis*-dominated patches (average ± SD). * indicates significant difference between patch types within each soil fraction.

The geographic range of associated species

Species associated with each patch type had highly variable geographic ranges. Two species were left out of this analysis due to the lack of a distribution map or a reliable species name (Table 1.). Among species associated with the shortgrass steppe dominant, *B. gracilis*, *Sphaeralcea hastulata*, *Chamaesyce serrula*, *Ipomoea costellata*, and *Bouteloua barbata* occur throughout the Chihuahuan desert region with little extension into the Great Plains. Other species associated with *B. gracilis*-dominated patches, such as *Solanum elaeagnifolium*, *Euphorbia dentata*, *Chamaesyce serpyllifolia*, are widespread in both the Chihuahuan desert and the Great Plains, including the shortgrass steppe. Similarly, among the species associated with the Chihuahuan Desert dominant, *B. eriopoda*, *Sporobolus flexuosus*, *Sphaeralcea wrightii*, *Psilostrophe tagetina* can be considered Chihuahuan desert species since they are rare or do not occur in the Great Plains, yet they extend south into Mexico where the Chihuahuan Desert lies. Other species associated with *B. eriopoda*-dominated patches, such as *Gutierrezia sarothrae*, *Salsola tragus*, *Machaeranthera pinnatifida*, and *Aristida purpurea*, are widespread throughout both regions.

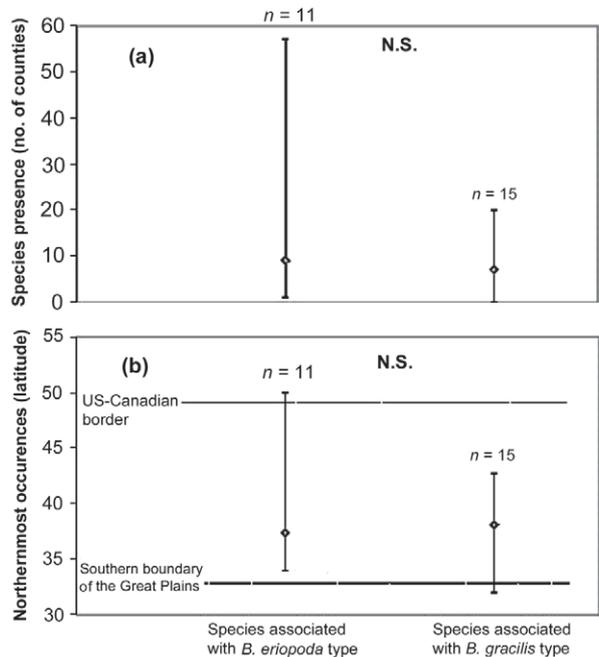


Fig. 3. Characteristics of the geographic distribution of species associated with *B. eriopoda*- vs. *B. gracilis*-dominated patches: (a) number of counties in the shortgrass steppe where at least a species occurs, and (b) latitude of northernmost occurrence of species in the Great Plains (median, interquartile range; N.S. = not significant).

The two groups of species associated with the two patch types at the transition zone (Table 1) did not differ significantly in the number of counties they occurred in within the shortgrass steppe (Fig. 3a). Number of counties by species was highly variable, especially for species associated with *B. eriopoda*-dominated patches. The two groups of species based on patch type did not differ either in the northern limit of their distributions within the Great Plains (Fig. 3b).

Of the 16 and 12 species that were associated with *B. gracilis*- and *B. eriopoda*-dominated patches at the transition zone, 9 (56%) and 7 (58%) species, respectively, were encountered in a study at a typical Chihuahuan desert grassland site in southern New Mexico (Hochstrasser et al. 2002).

Discussion

Differences between patch types of the biome transition zone

Patches dominated either by *Bouteloua gracilis* or by *B. eriopoda* differed considerably in species and life form composition; 28 of 52 species and 4 of 6 life forms showed preference for one of the two patch types. These results show that patch types of biome transition zones, which are generally defined and treated on the basis of the dominant species or life forms (Gosz 1993; Timoney et al. 1993; Anand & Li 2001), may also differ in species and life form composition. This compositional difference between patch types may be even greater at biome transition zones where vegetation types of different physiognomy meet (e.g., forest-steppe, Scanlan 1981; Wesser & Armbruster 1991). The presence and interspersed of compositionally different patch types results in the high β -diversity predicted for biome transition zones (Neilson et al. 1992; Risser 1995).

Differences in species and life form composition indicate that the two patch types provide different habitats for many subordinate species, either due to differences in the dominant species or to differences in abiotic factors, such as soil texture. *Bouteloua gracilis* is a slow-growing, long-lived bunchgrass with an ability to begin growth earlier in the growing season than *B. eriopoda* (Wright & Van Dyne 1976; Coffin & Lauenroth 1990; Peters 2002a). Also, *B. gracilis* has less canopy cover and aboveground biomass than *B. eriopoda* (Kröel-Dulay 1998; Peters 2002b). The mostly C3 (cool season) perennial forbs and shrubs may favor *B. eriopoda*-dominated stands over *B. gracilis*-dominated ones because of the smaller temporal overlap in water use. By contrast, the mostly C4 (warm season) annuals may be less successful in *B. eriopoda*-dominated stands be-

cause *B. eriopoda* also concentrates its activity in the warmest months and reaches higher cover as compared to *B. gracilis*.

Differences in soil texture may affect soil water availability by depth with resulting effects on species distributions and life form composition in semi-arid and arid grasslands (Noy-Meir 1973; Wondzell & Ludwig 1995). Fine-textured soils have higher water-holding capacity, and since precipitation is low, less water penetrates into deeper soil layers compared to coarse-textured soils. Thus, higher clay and lower rock content in *B. gracilis*-dominated patches may favor shallow-rooting annuals, whereas coarse-textured soils in *B. eriopoda*-dominated patches may be more favorable for deep-rooting perennial forbs and shrubs (Noy-Meir 1973). Although soil texture differences are relatively small between patch types, the influence of soil texture on life form composition is further supported by the significant correlations found between clay content and species richness of annuals and deep-rooting perennials within each patch type. Thus, both species-specific differences between the dominants and soil texture differences may contribute to generate differences in species and life form composition between the two patch types at this biome transition zone.

Although soil texture differs significantly between the two patch types, the high overlap indicates that soil texture only partially explains the segregation of the dominant species into patch types. The inverse-texture hypothesis suggests that under semi-arid climate fine-textured soils provide less available water for plant growth compared to coarse-textured soils due to the increased evaporation (Noy-Meir 1973; Sala et al. 1988). The more frequent occurrence of *B. gracilis*-dominated patches on functionally drier (more clay, less rock) habitats suggests that its dominance at the biome transition zone and its further expansion into the more arid areas is not directly limited by water shortage. Other factors such as precipitation seasonality, temperature, increased competition, or different disturbance regime may be responsible for the shift from *B. gracilis* dominance to *B. eriopoda* dominance (Gosz & Gosz 1996; Fields et al. 1999; Minnick & Coffin 1999; Peters 2000).

Patch types and the adjacent biomes

The groups of species associated with each patch type did not differ in their geographic range and in their distribution in the shortgrass steppe. Also, a similar proportion of species from the two species groups occurred at a Chihuahuan desert grassland site in southern New Mexico. These results show that there is a similar degree of overlap in species composition between any of the patch types – *B. gracilis*- or *B. eriopoda*-domi-

nated – and any of the adjacent biomes – shortgrass steppe or Chihuahuan desert, whether their dominant species is the same or different. This indicates that the similarity between patch types and the corresponding biomes (Gosz 1993; Risser 1995) is limited for the dominant species, and does not hold for subordinate species composition. Biomes may have characteristic floristic composition (Cox & Moore 1985; Begon et al. 1996), but subordinate species occurring at this transition zone were found to be associated individually to patch types, independently from their geographic range and affinity to the adjacent biomes.

Bestelmeyer & Wiens (2001) found similar distribution patterns for ant species at the same biome transition zone. The preference of ant species for grassland type (*B. gracilis*- vs. *B. eriopoda*-dominated) was not related to the occurrence of these species at a shortgrass steppe or a Chihuahuan desert site. This suggests that the distribution patterns at biome transition zones may be similar across different taxonomic groups.

Whether the observed pattern in species composition is valid for other broad-scale transition zones may depend on the contrast between adjacent biomes. At a grassland-grassland, forest-forest, or even grassland-shrubland transition zone where habitat quality of patch types may be similar, species are likely to show individualistic association patterns – as found in our case – or may in general show low affinity to patch types (Stohlgren et al. 2000). By contrast, at transition zones where the two dominant species or life forms have sharply differential effects on habitat quality, subordinate species may maintain their affinity to the broad-scale vegetation types. Species, for instance, that are characteristic of a forest biome ('forest species') are usually associated with forest patches within a forest-steppe zone as well (Scanlan 1981; Wesser & Armbruster 1991).

Biome transition zones are predicted to become biome interiors as a result of changes in climate that shift the distribution of the dominant species (Neilson 1993; Risser 1995). Previous studies of the two dominant *Bouteloua* species showed their sensitivity to climate at this transition zone (Minnick & Coffin 1999; Peters 2000). Thus, areas in central New Mexico that are currently a transition zone between the shortgrass steppe and the Chihuahuan desert may become a biome interior if climate changes sufficiently to shift species dominance patterns. It is unknown how patterns in species composition will be affected by such changes, but identifying current patterns is a first step in order to make these predictions. The results presented in this study emphasize the importance of studying subordinate species compositions since they may have different current patterns and may respond differently compared to the dominant species.

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