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Ecological restoration needs derived from reference conditions for a semi-arid landscape in Western Colorado, USA

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Abstract

Semi-arid ecosystems cover tens of millions of hectares in the Intermountain West of the United States, and most have altered plant communities due to land use, especially livestock grazing. Thus, relatively unaltered "reference" plant community information is needed to guide restoration. Plant communities were sampled over a large (~600 000 ha) semi-arid landscape in western Colorado, within piñon–juniper woodlands, sagebrush shrublands, and grasslands, and over conditions ranging from relict areas without livestock grazing to heavily utilized areas. Ordination was used to group samples into ranked categories of ecological condition within 18 communities, and means–tests and other techniques were used to identify ecological differences among ranks across vegetation types. With few exceptions, grass and forb cover, biological soil crust cover, and species diversity declined concomitant with ranks representing increasingly degraded conditions, while non-native species cover was variable among ranks. Landscape-level species abundance patterns also differed significantly among ranks, with herbaceous species generally exhibiting less constancy and cover within degraded samples compared to samples of reference quality. These semi-arid ecosystems will require both active (e.g., reseeding) and passive (grazing management) restoration approaches, at local- and landscape-levels, respectively, if the goal is to restore native plant composition and abundance.
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1. Introduction

Arid and semi-arid ecosystems cover tens of millions of hectares in the Intermountain West of the USA (Barbour and Billings, 2000) and are the focus of substantial restoration interest, as land-use practices have altered community diversity, structure, function, and extent (DiTomaso, 2000; Hemstrom et al., 2002; Nabhan et al., 2004). Many of these ecosystems were managed with a past emphasis on improving forage for livestock (e.g., Wasser, 1942). However, management interests have broadened to include restoring these ecosystems to

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within their ranges of natural variability where feasible (Nabhan et al., 2004), including reestablishing natural disturbance regimes and native species diversity (Flather and Sieg, 2000; Ford et al., 2004; Weltz et al., 2003).

Piñon–juniper woodlands, sagebrush shrublands, and grasslands, the focus here, dominate semi-arid ecosystems in the Intermountain West and are often targets of restoration (e.g., Brockway et al., 2002; Wrobleski and Kauffman, 2003). Concern over these ecosystems arose around A.D. 1900 as reduced grass and increased erosion from unregulated grazing became apparent, especially in the southwestern US (Leopold, 1924; West, 2003). However, sagebrush was long viewed as an undesirable shrub, and sagebrush ecosystems have only recently become a restoration focus, due in part to an increasingly imperiled obligate fauna (Welch, 2005). Sagebrush ecosystems are fragmented and reduced in extent from land-use conversion and roads, clearing for livestock, and fire-driven conversion to non-native annual grasses (Hemstrom et al., 2002; Welch, 2005). Piñon–juniper restoration has typically emphasized tree clearing and thinning (e.g., Brockway et al., 2002), as grazing and fire exclusion were thought to have allowed tree invasion into shrublands and grasslands and created denser stands unnaturally susceptible to stand-replacing fires, insect outbreaks, soil erosion, and biodiversity loss (Davenport et al., 1998; Harper et al., 2003; Miller and Tausch, 2001). However, where dense piñon–juniper woodlands with stand-replacing fire regimes are within the range of natural variability (Baker and Shinneman, 2004; Floyd et al., 2004; Romme et al., 2003), thinning and clearing are ecologically inappropriate and unlikely to restore altered plant communities.

Despite grazing by extinct Pleistocene fauna (Martin, 2005), many marginally productive semi-arid communities likely evolved without large herds of hoofed, ungulate grazers, and are especially vulnerable to livestock grazing (Mack and Thompson, 1982). Livestock grazing may interact with pervasive non-native species and (1) reduce native plant species abundance (Booth et al., 2003; Vesk and Westoby, 2001); (2) damage biotic components that support native plants, including biological soil crusts (Belnap et al., 2001) and stand structures (Miller et al., 2000); and (3) alter natural disturbance regimes, water and nutrient cycles, and light availability (Brooks et al., 2004; DiTomaso, 2000; Neff et al., 2005). These changes can create alternative successional pathways that surpass biotic and abiotic thresholds, making restoration difficult (Laycock, 1991; Westoby et al., 1989).

Before restoration can be effective, research is needed to understand how woodland and shrubland plant composition and diversity have been affected by land use. Reference communities may serve as invaluable sources of information in this process (White and Walker, 1997). Potential reference areas include livestock exclosures, protected areas (e.g., national parks) with land-use restrictions, and relict sites unaffected by direct land uses. Yet, protected areas may provide imperfect representations of native plant communities if incompletely recovered from past land uses, such as livestock grazing (Anderson and Inouye, 2001; Neff et al., 2005), and may even remain in unnatural stable states (Westoby et al., 1989). Relict areas are rare, usually steep-sided mesas or other topographically isolated features that preclude livestock access, and may have atypical environmental conditions, such as thin, rocky soils (Guenther et al., 2004). Despite these limitations, protected areas and relicts offer the best opportunities to determine native plant community conditions within otherwise extensively altered landscapes and thus are invaluable sources of ecological information.

In this research, a large, semi-arid landscape in western Colorado was sampled across a gradient of conditions, from highly utilized to relict. The goals were (1) to find and study reference areas across a large semi-arid landscape to further scientific understanding and guide ecological restoration; (2) to analyze species composition and diversity changes along a degradation gradient; and (3) to investigate our hypothesis that similar patterns of degradation occur among disparate semi-arid communities, resulting in similar restoration needs among these communities.

2. Study area and methods

2.1. Study area

The Uncompahgre Plateau is in western Colorado (Fig. 1), where the Colorado Plateau meets the Southern Rockies, and is dissected by many canyons, including Unaweep Canyon which forms the northern border of the 593 038 ha primary study area. Three of the sampled reference areas were just outside this primary area (Fig. 1). Geologic substrates include sandstone, siltstone, mudstone, and shale formations of the Cretaceous,

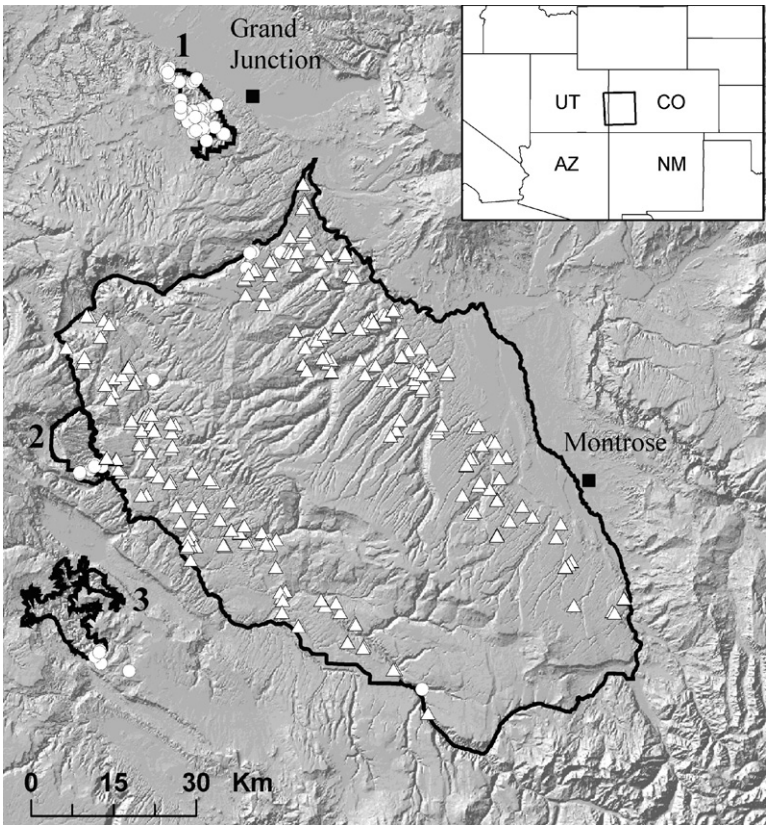


Fig. 1. The primary study area of the Uncompahgre Plateau, outlined in black. Smaller outlined areas with numbers refer to the three reference areas outside the primary study area: (1) Colorado National Monument, (2) Sewemup Mesa Wilderness Study Area, and (3) Bull Canyon Wilderness Study Area. Triangles represent random/opportunistic sample sites; circles are reference area sites.

Jurassic, and Triassic, and occasional Precambrian outcrops (Scott et al., 2001). Sandy soils are generally shallow to moderately deep and well drained (USDA Natural Resource Conservation Service, 1995), but patches of deeper eolian, colluvial, and alluvial soils may occur on level to gentle slopes and along cliff- and canyon-bottoms, while high clay content is common in soils of the slope-forming Morrison formation and some Cretaceous formations (Scott et al., 2001). Extensive biological soil crusts can develop on stable soils from all substrates, regardless of slope angle, but especially on shallow, fine-textured, and calcareous soils (Belnap et al., 2001).

A semi-continuous zone of piñon–juniper woodlands (*Pinus edulis*–*Juniperus osteosperma*), with scattered grasslands and shrublands, occurs between 1800–2300 m elevation on ~240 000 ha of the primary study area. Between 1400–1800 m elevation, scattered woodlands occur in a mosaic with semi-desert grasslands and shrublands (e.g., sagebrush—*Artemisia tridentata*). Winters are cool and summers typically hot, with mean July temperatures reaching 34 °C at low elevations. Precipitation increases from ~20 cm per year at the lowest elevations to >40 cm at upper elevations of the piñon–juniper zone (Western Regional Climate Center, 2005), with peaks occurring in late summer and early fall because of convective and monsoon thunderstorms. Moisture retention is influenced by aspect, with northeast-facing slopes receiving less insolation (Beers et al., 1966).

The Ute Indians used the Uncompahgre Plateau for hunting, fuel-wood gathering, and collection of piñon nuts and other foods, possibly since A.D. 1100, but had few permanent settlements (Cassells, 1997; Simmons, 2000). After EuroAmerican settlement in 1881, intense and unregulated livestock grazing persisted until the 1940s, followed by extensive clearing of woodlands to increase livestock forage. There is now widespread

interest in restoring the region's ecosystems to their ranges of natural variability (Uncompahgre Plateau Project, 2005). Most of the Plateau is publicly owned (~75% of the study area), managed primarily by the US Forest Service and Bureau of Land Management.

2.2. Site selection and sampling design

A total of 302 sites was sampled for this study, mostly on Bureau of Land Management lands, including 123 stratified-random sample sites, 116 "companion" sites, and 63 potential reference sites. A geographic information system (GIS) was used to produce the random sample stratified by slope, aspect, elevation, geologic substrate, and vegetation type, and a GPS was used to navigate to sites. On occasion, a site did not match expected strata, and an alternative site that best matched the original criteria was located nearby. Once a site was sampled, a second "companion" site was opportunistically sampled nearby (<500 m) within a different environmental setting or vegetation type (if available), a necessity given the large and relatively inaccessible study area. Sites were sampled during summers of A.D. 2002–2004 to span year-to-year floristic variation. During January 2002–August 2004, western Colorado drought conditions were "severe" to "extreme" (NCDC, 2007); thus, moisture availability was similar for each sample period. In nine main reference areas sampled in 2004, selected based on evidence of light or restricted land uses (Table 1), sites were sampled that matched the random sample environments but avoided localized areas with obvious degradation (e.g., trampling, woodcutting, livestock-grazing evidence such as pedestaled plant bases) if present.

An estimate of percent canopy cover was made for each vascular plant species within a 20 m × 50 m (0.1 ha) plot. Plants in this semi-arid environment were commonly discrete, allowing their cover to be summed using a meter stick to estimate areas of patches, during a systematic traverse of the plot. Total cover for each species was rounded: trace (<0.5%), 1% increments up to 20% cover, and 5% increments above 30% cover. Percent cover of biological soil crust, rock, and litter was similarly estimated. Evidence of land use, including past treatments (e.g., thinning, chaining), firewood cutting, livestock grazing, or recreation, was also recorded. Slope, aspect, elevation, and geologic substrate were recorded, and photographs were taken. Plants not

Table 1
List of potential reference areas with descriptions of key reference characteristics

Reference area	Characteristics
Sewemup Mesa WSA	Roadless, steep-sided mesa with few access points for livestock to limited portions of the plateau. Most of the plateau is considered a true relict that has never been grazed by livestock
Jack's Canyon	Level area on the rim of Unaweep Canyon used mainly as seasonal stock driveway
Gibler Mesa	Steep sided mesa top with no road-access and only a few rugged access points for livestock. Uncertain if true relict, but no signs of cattle grazing when sampled
Pine Hill WSA	Rugged roadless area; portions far from water source for livestock; lightly grazed
Iron Springs Mesa	Long narrow mesa top with no water source at distant end; portions lightly grazed
Dominguez Canyon WSA	Large, rugged, roadless area with portions heavily grazed, but with some remote areas without accessible water
Bull Canyon WSA	Roadless canyon with many large, level benches between canyon rim and canyon bottom that are difficult for livestock to access and, thus, some portions lightly or never grazed
Devil's Canyon	Roadless canyon, now partially contained within a federally protected Wilderness Area, that has not been actively grazed since the early 1980s
Colorado National Monument	Currently owned and protected from livestock grazing by the US National Park Service. Livestock grazing was mostly removed after park designation in 1915 and fenced out of most areas by the 1930s, with only few exceptions made for short-duration livestock trail drives through historic and limited routes until the 1980s. Bison were introduced in the 1920s and removed by the early 1980s. Prior to removal, grazing by bison was limited primarily to the canyon bottoms, while livestock access was more variable. However, many remote mesa tops, canyon benches, and other rugged areas with no accessible water sources were lightly or never grazed by livestock

Wilderness Study Area (WSA) refers to a roadless area managed by the US Bureau of Land Management and that is being considered for federal protection under the US Wilderness Act.

identified to species were pressed for laboratory identification. Some specimens could be identified only to genus (3% of total) and fewer (0.4% of total) only to family or group (e.g., native perennial grass). Nomenclature follows the PLANTS database (USDA Natural Resources Conservation Service, 2005).

2.3. Statistical analysis

The analysis included five steps: (1) dividing sites from the pooled dataset (random, opportunistic, and reference sites) into major vegetation types, based on percent cover threshold values for dominant and subdominant species (Table 2); (2) using ordination analysis to divide these major types into narrower plant communities; (3) identifying reference conditions within each community using known reference sites (and similar sites nearby in ordination space), and ranking all sites relative to reference conditions; (4) comparing key community attributes (e.g., species richness) among ranks, and (5) testing whether differences in ranks could be due to environment, rather than land use.

Within each major vegetation type defined in step 1 (Table 2), non-metric multidimensional scaling (NMS; Kruskal, 1964; Mather, 1976) in PC-ORD for Windows, Version 4.35 (McCune and Mefford, 1999) was used in step 2. Some pre-processing occurred first, including: (1) temporarily omitting the consistent overstory shrub or tree dominating each major vegetation type, to focus on understory degradation; (2) square-root transforming percent cover and omitting species in <5% of plots, to reduce skew and lower the coefficient of variation among species totals; and (3) calculating site similarities using Sørenson's distance (Greig-Smith, 1983), after which sample sites >3 s.d. from mean distance within each community were examined and excluded from analysis, as outliers, if compositionally different from the rest of the community.

NMS, which is considered superior for ecological applications because of its effectiveness with nonlinearities and noise (Urban et al., 2002), iteratively reduces "stress" in rank correlation between distances in multidimensional ecological space and reduced-dimension ordination space. Rank correlation is

Table 2
Major vegetation types to which sites were assigned before the ordination analysis: given below each vegetation type (e.g., Grassland VT1.0) are predetermined target percent cover threshold values for key species and species groups in each vegetation type and, further below, the mean percent cover values for key species and species groups after all sites were assigned to a vegetation type

	Major vegetation type–name (code)				
	Grassland (VT1.0)	Wyoming big sagebrush (VT2.0)	Black sagebrush (VT3.0)	Piñon–juniper savanna and woodland (VT4.0)	Piñon–juniper mixed mountain shrub (VT5.0)
	Cover % target criteria before delineation				
	<10% tree; <5% black sagebrush; <5% big sagebrush; <25% all shrub	<10% tree; >5% Wyo. sagebrush; <15% other shrub	<10% tree; >5% Black sagebrush; <15% other shrub	>10% tree; <5% mixed mountain shrub	>5% tree; >5% mixed mountain shrub; <5% sagebrush
	Mean values after delineation				
No. sites	39	41	15	121	64
Mean cover %					
Grass	35.40	23.84	11.17	7.31	6.98
Saltbush	2.30	0.67	1.01	0.41	0.00
Black sagebrush	0.79	0.09	25.00	1.04	0.58
Wyo. big sagebrush	0.42	23.05	0.67	0.93	0.27
All sagebrush	2.17	23.21	25.67	2.58	1.10
Mixed mtn. shrub	0.01	0.06	0.01	0.57	14.40
All shrub	9.22	25.89	33.07	5.63	19.30
Piñon–juniper	1.32	2.06	1.63	24.25	33.01

then used to estimate the variance explained by the ordination axes (McCune and Grace, 2002). We performed multiple ordination runs ($n \geqslant 40$) with random starting configurations and 6-dimensional space, followed by Monte Carlo tests to determine if final stress was significant compared to stress from 50 runs of a randomization of the data (McCune and Grace, 2002). An optimal ordination configuration is reached by selecting the highest number of dimensions with stress less than that obtained in 95% of randomized runs and the lowest stress statistic from the real data.

After we examined the resulting ordination diagrams, clusters of sites in ordination space were assigned to communities based primarily on similarities in dominant species cover, elevation, and geologic substrate, ascertained from overlays of these attributes on the ordination diagrams. A multi-response permutation procedure (MRPP) was then used to test if communities were statistically distinct. MRPP is a multivariate, non-parametric test that compares distance measures between selected and randomized sets of groups from the same dataset (Mielke and Berry, 2001).

In step 3, within each community, reference Rank 1 was assigned to clusters of sites that contained known reference sites separated in ordination space from other sites. Other clusters at increased distance in ordination space from Rank 1 sites were sequentially assigned Ranks 2 and 3, effectively along gradients of increasing degradation. The location of potential reference sites in ordination space guided this process, but there was no requirement to assign these sites to Rank 1 (e.g., if a site did not cluster with other reference sites), and random/companion sites could also be assigned to any rank.

In step 4, two main approaches were used to evaluate how the ecological conditions in the reference ranks differed. First, reference species were identified using indicator species analysis (ISA), which combines relative abundance and frequency to derive an indicator value for each species within groups, and then determines the significance of those values using a Monte Carlo test of no difference among the groups (Dufrêne and Legendre, 1997). Native species were tested at $\alpha = 0.10$. Characteristic reference native grass species were further identified within each community as those with mean cover $\geqslant 5\%$ in Rank 1 sites, more than 50% constancy across Rank 1 sites, and with more than a 50% increase in mean cover in Rank 1 sites vs. non-reference sites (Ranks 2 and 3).

Second, species abundance and diversity, as well as cover of species groups and biological soil crust, were compared among ranks. For a visual comparison, log-transformed species abundance was plotted, based on total cover (m^2) against species sequence (Magurran, 1988) and constancy among plots (Urban et al., 2002). These graphs were created for the final 64 Rank 1 sites and 64 randomly selected Rank 3 sites (after final rank designations), with equal numbers of sites among each vegetation type for each rank. For a statistical comparison, Fisher's protected least significance difference (LSD) was used to test differences in the means ($\alpha = 0.05$) among reference ranks for species richness (total and by species groups), species diversity (Shannon index), percent cover by species groups (graminoid, forb, non-native), and percent cover of biological soil crust. Reference-ranked groups within communities often had few sites, so variable means for each reference rank were pooled to the level of major vegetation types for statistical analysis. To pool data with different ranges, data were relativized by the maximum value for each variable within each community. After pooling, data had non-normal distributions and heterogeneous variances and were rank-transformed (McCune and Grace, 2002), as other transformations (e.g., arcsine square-root) were insufficient. Relativization at the community level followed by rank transformation at the level of major vegetation type allowed valid comparisons among community types with different compositions.

In step 5, multiple ordinal logistic regression (OLR) was used to test the alternative hypothesis that reference ranks were determined by environment rather than degradation. Geologic substrate was used as a categorical predictor (sandstone, shale, and "other"), while slope (degrees), elevation (m), and cosine-transformed aspect (Beers et al., 1966) were used as continuous predictors (covariates) in the models. Best models were derived using backward selection, sequentially removing covariates and categorical variables, and performing log-likelihood tests of the nested models using deviation χ^2 differences. If significant environmental predictors were found, we then explored whether a narrow range of environmental conditions within reference areas may have created a bias in the final OLR model, rather than environmental variables truly influencing reference ranks. To test this, a subset of sample sites was selected that specifically matched the environments of the reference ranks, and mean values for species richness, graminoid percent cover, and forb

percent cover were compared again among reference ranks in this subset, using Fisher's LSD to re-test for significant differences.

3. Results

3.1. Overview of classification results

After removal of 22 sites (including 2 reference sites) representing communities with sample sizes too small for analysis, the remaining 280 sites collectively contained 339 species, including 5 native trees, 44 shrubs or small trees, 222 native forbs or sub-shrubs, 26 native graminoids, 9 native cacti, 9 non-native grasses, and 24 non-native forbs. Before final community classification, a preliminary NMS ordination allowed subdivision of the large number of sites in the piñon–juniper woodland vegetation type (VT4.0) into three subtypes containing grass–forb, sagebrush, and sparse mountain shrub understories. The NMS ordinations of these subtypes and the other 4 vegetation types settled on 3-dimensional space solutions, with Monte Carlo tests significant at $\alpha = 0.02$ and, depending on the vegetation type, with 65.3–79.9% of the variation in the original multidimensional space explained (Table 3). The ordination results are presented (Fig. 2) with the first axis explaining the greatest variance and, with the exception of VT2.0, the second axis explaining the second highest variance, or nearly so (i.e., when R^2 values between remaining axes were within 0.04).

After NMS ordination, overlays of dominant species and environmental variables onto ordination diagrams led to delineation of 18 communities: the grassland vegetation type (VT1.0) was divided into 2 (Fig. 2a); Wyoming big sagebrush (VT2.0) into 3 (Fig. 2b); black sagebrush (VT3.0) into 2 (Fig. 2c); piñon–juniper woodland (VT4.0) into 8 (Fig. 2d–f); and piñon–juniper/mixed mountain shrub (VT5.0) into 3 communities (Fig. 2g). These communities were significantly ($p < 0.001$) but modestly different from one another (Table 3). Primary biotic and abiotic community characteristics are provided in Supplementary material Appendix 1 (electronic version); refer to Shinneman (2006) for detailed descriptions.

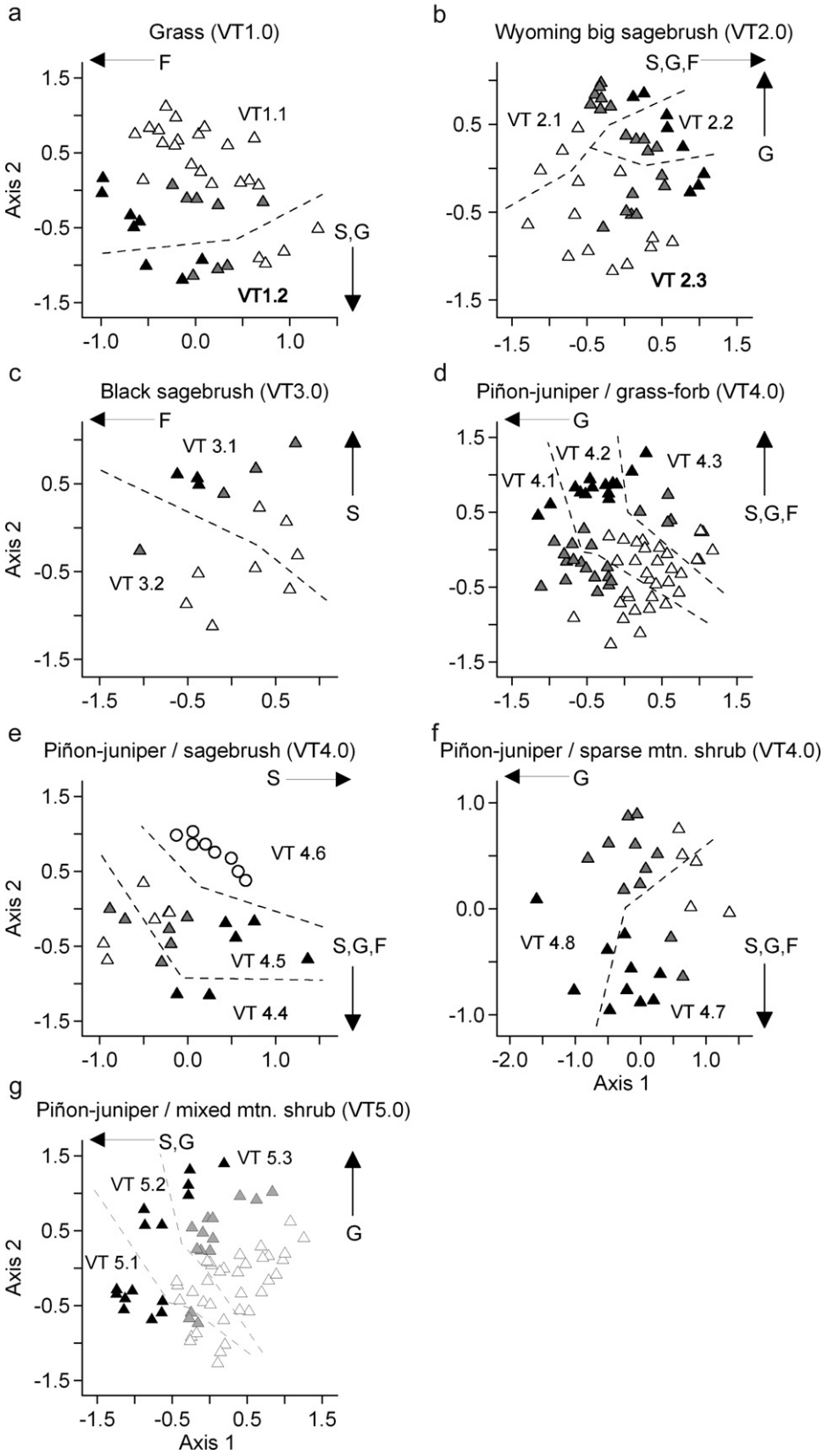
3.2. Reference ranks

Reference sites were typically clustered in a distinct part of the ordination space within each community, with increasingly distant sites lying along a gradient of reduced species richness, grass cover, or forb cover, as demonstrated by correlations ($R^2 \geqslant 0.2$) between these variables and one or more ordination axes (Fig. 2). Eight random/opportunistic sites in community VT4.6 (Fig. 2e) were not analyzed further, as this community contained no reference sites and ordination revealed no clear reference gradients (leaving 17 communities for

Table 3
The percentage of variation explained by the three-dimensional ordination solutions for each vegetation type, the Monte Carlo test of final stress values for each vegetation type, and the multi-response-permutation procedure (MRPP) results that were used to test for significant differences (based on Sørenson's distance) between each group of plots assigned to finer community levels

Vegetation type	% Variance explained by axes	Monte Carlo *p*-value	MRPP	
			A	*P*
Grassland (VT1.0)	78.1	0.0196	0.0819	0.0000
Wyoming big sagebrush (VT2.0)	71.0	0.0196	0.0956	0.0000
Black sagebrush (VT3.0)	75.8	0.0196	0.0577	0.0003
Piñon–juniper woodland (VT4.0)				
Piñon–juniper/grass–forb	65.3	0.0196	0.0494	0.0000
Piñon–juniper/sagebrush	79.2	0.0196	0.1023	0.0000
Piñon–juniper/sparse mixed mountain shrub	76.2	0.0196	0.0659	0.0000
Piñon–juniper/mixed mountain shrub (VT5.0)	79.9	0.0196	0.1056	0.0000

MRPP *A*-values represent an agreement statistic, with complete within-group homogeneity = 1.0, and with values less than 0.1 common in community ecology (McCune and Grace, 2002).


a
Grass (VT1.0)
F
VT1.1
S,G
VT1.2
Axis 2
b
Wyoming big sagebrush (VT2.0)
S,G,F
VT 2.1
VT 2.2
G
VT 2.3
c
Black sagebrush (VT3.0)
F
VT 3.1
S
VT 3.2
Axis 2
d
Piñon-juniper / grass-forb (VT4.0)
G
VT 4.2
VT 4.3
VT 4.1
S,G,F
e
Piñon-juniper / sagebrush (VT4.0)
S
VT 4.6
S,G,F
VT 4.5
VT 4.4
Axis 2
f
Piñon-juniper / sparse mtn. shrub (VT4.0)
G
VT 4.8
S,G,F
VT 4.7
Axis 1
g
Piñon-juniper / mixed mtn. shrub (VT5.0)
S,G
VT 5.3
VT 5.2
G
VT 5.1
Axis 2
Axis 1

analysis). Among the remaining 61 initial potential reference sites, 53 (86.9%) were assigned to Rank 1, and 8 (13.1%) to Rank 2. Of the remaining random/opportunistic sites ($n = 211$), 5.2% were assigned to Rank 1, 35.5% to Rank 2, and 59.2% to Rank 3. In total, 64, 83, and 125 sites were assigned to Ranks 1, 2 and 3, respectively. After all sites were assigned to ranks, one community had no sites in Rank 1 (VT3.2), one had no Rank 2 sites (VT5.2), and another had no Rank 3 sites (VT2.2), so a total of 16 communities were assigned to Rank 1 and least one other rank (see Fig. 2).

3.3. Ecological comparisons among reference ranks

Mean native graminoid percent cover was significantly higher in Rank 1 than in Rank 2 and 3 sites for all but the black sagebrush vegetation type, where it was higher than Rank 3 but not Rank 2 sites (Fig. 3a). In most cases, the differences were substantial. Rank 1 mean native graminoid percent cover was ~25% or greater in 12 of the 16 communities, and in 6 of 16 communities it was >50%. In contrast, with the exception of grassland communities, Rank 3 communities consistently had <10% mean grass cover, and in 8, mean grass cover was <1%. Based on ISA and reference comparison results (Supplementary material Appendix 2, electronic version), native bunchgrasses (*Achnatherum hymenoides*, *Elymus elymoides*, *Hesperostipa comata*, *Koeleria macrantha*, *Leymus salinus*, *Poa* spp., *Sporobolus cryptandrus*) were substantially more abundant in, or significantly indicative of, Rank 1 sites in 13 of 16 communities, as were warm-season grasses (*P. jamesii* and/or *B. gracilis*) in 6 of 16 communities.

Forb cover was also significantly different among ranks. Mean native forb cover was significantly higher in Rank 1 sites for all but the black sage and piñon–juniper/sagebrush types, for which there was no statistical difference (Fig. 3a). Differences were often substantial, as Rank 1 sites in 6 of 16 communities had 20% or higher forb cover, and Rank 1 sites in an additional 7 communities had at least 10% mean forb cover. In contrast, all Rank 3 sites had ~5% or less mean forb cover (Fig. 3a). Also, Rank 1 sites in 13 of 16 communities had at least one indicator forb, though indicator forb species were highly variable among communities (Supplementary material Appendix 2, electronic version).

Mean biological soil crust cover was significantly higher in Rank 1 sites compared to Ranks 2 and 3 for the grassland, Wyoming big sagebrush, black sagebrush, and piñon–juniper/grass–forb types, and higher in Rank 1 than Rank 3 in the piñon–juniper/sparse mixed mountain shrub type (Fig. 3a). Mean biological soil crust cover in Rank 1 communities approached 60% in Wyoming big sagebrush (VT2.1) and piñon–juniper/sparse mixed mountain shrub (VT4.7) communities, and across vegetation types, only three Rank 1 communities had <10% cover. No Rank 3 sites had >7% mean biological soil crust cover, and Rank 3 sites in 10 of 16 communities had <1%. The VT2.1 and VT4.7 communities, which had the highest mean biological soil crust cover within the Rank 1 sites, were essentially devoid of soil crust cover on Rank 3 sites. Among vegetation types, the piñon–juniper/ mixed mountain shrub communities stood out as relatively depauperate in biological soil crust cover, with ⩽11% mean cover irrespective of reference rank.

Mean percent cover of non-native species showed less clear or even inverse trends across ranks (Fig. 3a). Cover of non-natives was significantly higher in Rank 1 than Rank 3 sites for the two piñon–juniper mixed-mountain shrub types, higher than both Rank 2 and 3 sites in the piñon–juniper/grass–forb type, but not different from ranks 2 and 3 in the piñon–juniper/sagebrush and Wyoming big sagebrush types (though means for the latter two ranks differed). No significant difference was found among ranks for non-native cover in grassland and the black sagebrush types, though cover was higher in Rank 3 sites. Differences within the piñon–juniper communities (VT4.0 and 5.0), though significant, were small, as only 2 of 29 ranked groups (6.9%) had non-native cover values as high as 2–4%. In contrast, in sagebrush and the grassland vegetation

Fig. 2. Results of ordination of sample plots by seven major vegetation types/subtypes, with plant community types (e.g., VT1.2) separated by dashed lines. Reference ranks are indicated by black triangles for Rank 1 sites, gray triangles for Rank 2 sites, and white triangles for Rank 3 sites. Circles for VT4.6 indicate that no reference ranks were assigned. Letters with arrows indicate key variables positively or negatively correlated ($R^2 \geqslant 0.2$) with the ordination axes (based on direction of arrows): G = grass percent cover, F = forb percent cover, and S = species richness.

types (VT1.0, 2.0, 3.0), non-native cover was commonly >2% (11 of 19, or 57.9% of ranked groups) and reached 20% in two Rank 3 sites (Fig. 3a).

Mean native species richness significantly increased from Ranks 3 to 1 in all but the piñon–juniper/sagebrush type, in which Rank 1 sites had a higher mean than both Ranks 2 and 3, and the black sagebrush type, where there was no difference (Fig. 3b). Mean forb species richness was significantly higher in Rank 1 than Ranks 2 and 3 across all vegetation types except black sagebrush, where it was superior to Rank 3 but not Rank 2. Mean graminoid species richness was significantly higher in Rank 1 compared to Ranks 2 and 3 sites for grassland and Wyoming big sagebrush types, and higher than Rank 3 sites for all remaining vegetation types except black sagebrush, where there was no significant difference (Fig. 3b). Shannon diversity also had a significantly higher mean in Rank 1 sites for the grass, Wyoming big sagebrush, piñon–juniper/grass–forb, and piñon–juniper/sagebrush types, and a higher mean in Rank 1 than Rank 3 sites in the two piñon–juniper mixed mountain shrub types. Only black sagebrush had no significant difference in mean Shannon diversity among ranks.

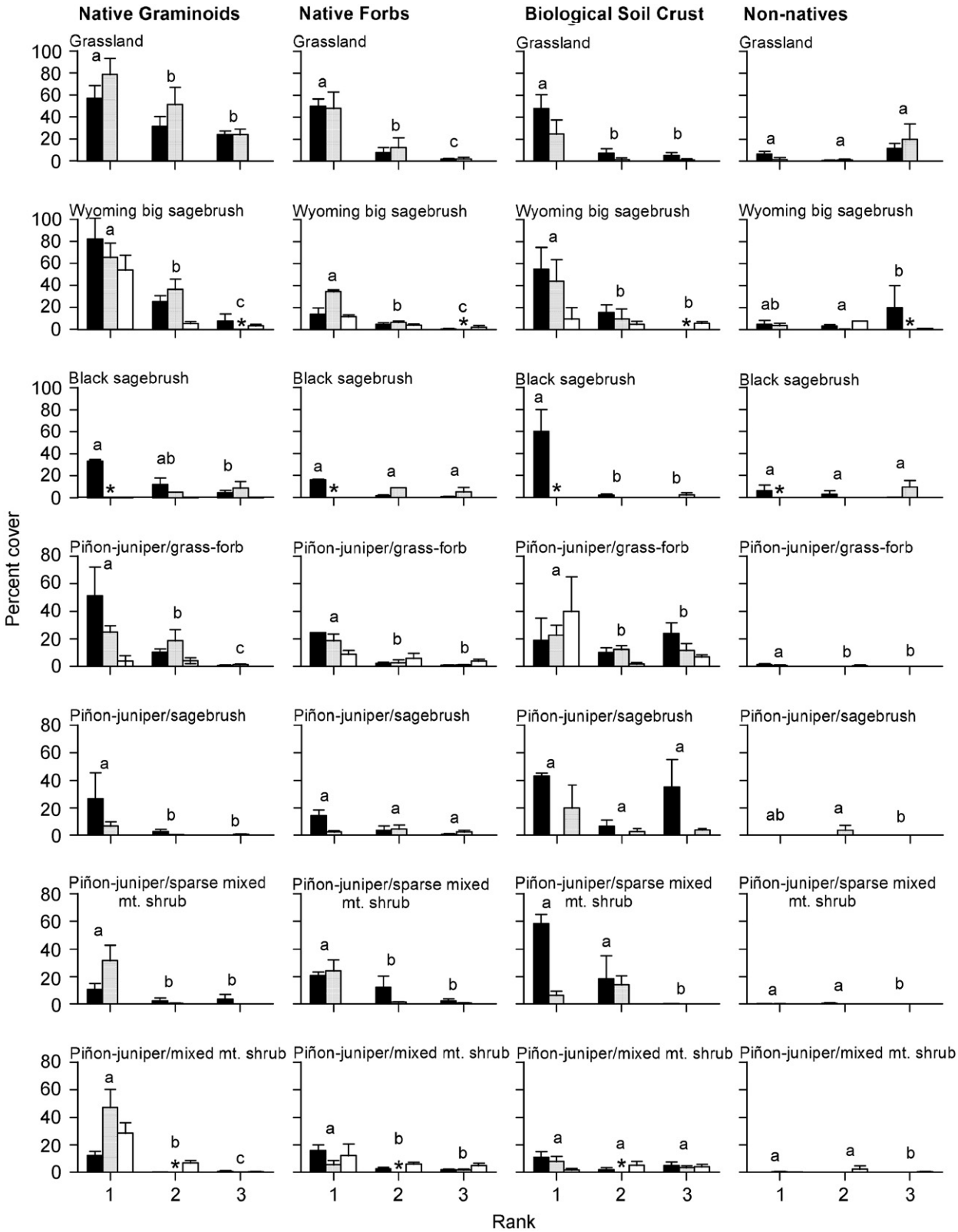
Mean richness values among all community types within Rank 1 sites were generally similar, as were mean values for Rank 3 communities (Fig. 3b). If mean richness values for each rank are further averaged across all community types, the differences between Ranks 1 and 3 sites represent a 55% decrease in overall species richness, 63% decrease in number of graminoids, and 67% decrease in number of forbs. The greatest species loss among the communities is the piñon–juniper/Wyoming big sagebrush type (VT4.4). This community not only had the highest mean richness of Rank 1 sites, but also the greatest reduction in richness between Ranks 1 and 3 sites, with an 80% decrease in overall species richness, 94% decrease in number of graminoids, and 96% decrease in number of forbs, as well as being the most depauperate in total native species among all communities (Fig. 3b).

Species abundance curves for native species in all vegetation types for the 64 Rank 1 sites and an equal number of Rank 3 sites demonstrated two distinct patterns (Fig. 4a). The curve for Rank 1 sites represents 245 native species and exhibits a nearly log-normal distribution, while the curve for Rank 3 sites represents 158 native species and resembles a log series distribution of abundance, indicating a higher proportion of uncommon species (see Magurran, 1988). Plotting cover area vs. frequency for each species also demonstrates fundamental differences, as Rank 1 sites (Fig. 4b) have greater species constancy and coverage relative to Rank 3 sites (Fig. 4c), especially for forbs and graminoids. For shrubs, coverage does not vary greatly between the two ranks, but constancy is higher for Rank 1 sites (Fig. 3b and c). Overall, Rank 1 sites contained 112 species not contained in Rank 3 sites, including 93 forbs, 8 shrubs, 8 grasses, 2 trees, and 1 cactus. Of these, 75% occurred in less than 5% of Rank 1 sites, mostly with trace or small percent cover (<2%) per plot, indicating a suite of species that exist irregularly across reference landscapes at low local abundance levels.

3.4. Environment influences on reference ranks and conditions

The OLR results identified some environmental variables as significant predictors of reference ranks for 4 of the 7 major vegetation types/subtypes (Table 4), including: (1) shale substrates substantially increased the odds of a site being assigned to better ranks in black sagebrush (VT3.1 and 3.2); (2) northeast aspect modestly decreased the odds of a site being assigned a superior reference rank in piñon–juniper/sagebrush communities (VT4.4 and 4.5); (3) a less steep slope and northeast aspect substantially increased the odds of superior reference ranks in the piñon–juniper/sparse mixed mountain shrub communities (VT4.7 and 4.8); and 4) a northeast-trending aspect substantially influenced better ranks in the piñon–juniper/mixed mountain shrub (VT5.1, 5.2, 5.3) communities.

However, controlling for environmental differences suggests trends among ranks are still valid. Inadequate sample sizes limited testing to 5 of these 9 communities: VT4.7, 4.8, 5.1, 5.2, 5.3. When a subset of sites in these five was limited to northeast-trending aspects (cosine-transformed aspect $\geqslant 1$) for both reference and non-reference sites ($n = 55$), Rank 1 sites had significantly ($\alpha = 0.05$) higher means than Rank 2 and 3 sites for native species richness (Rank 1, 2, and 3 means = 32.5, 23.4, 17.7, respectively), percent forb cover (Rank 1, 2, and 3 means = 14.5, 5.0, 2.9, respectively), and percent grass cover (Rank 1, 2, and 3 means = 19.5, 4.3, 1.3, respectively). In addition, there was no significant difference in mean cosine-transformed aspects among the 3 ranks (Rank 1, 2, and 3 means = 1.6, 1.7, 1.7, respectively) within this subset at $\alpha = 0.05$, suggesting the


Native Graminoids
Native Forbs
Biological Soil Crust
Non-natives
Grassland
Wyoming big sagebrush
Black sagebrush
Piñon-juniper/grass-forb
Piñon-juniper/sagebrush
Piñon-juniper/sparse mixed mt. shrub
Piñon-juniper/mixed mt. shrub
Percent cover
Rank

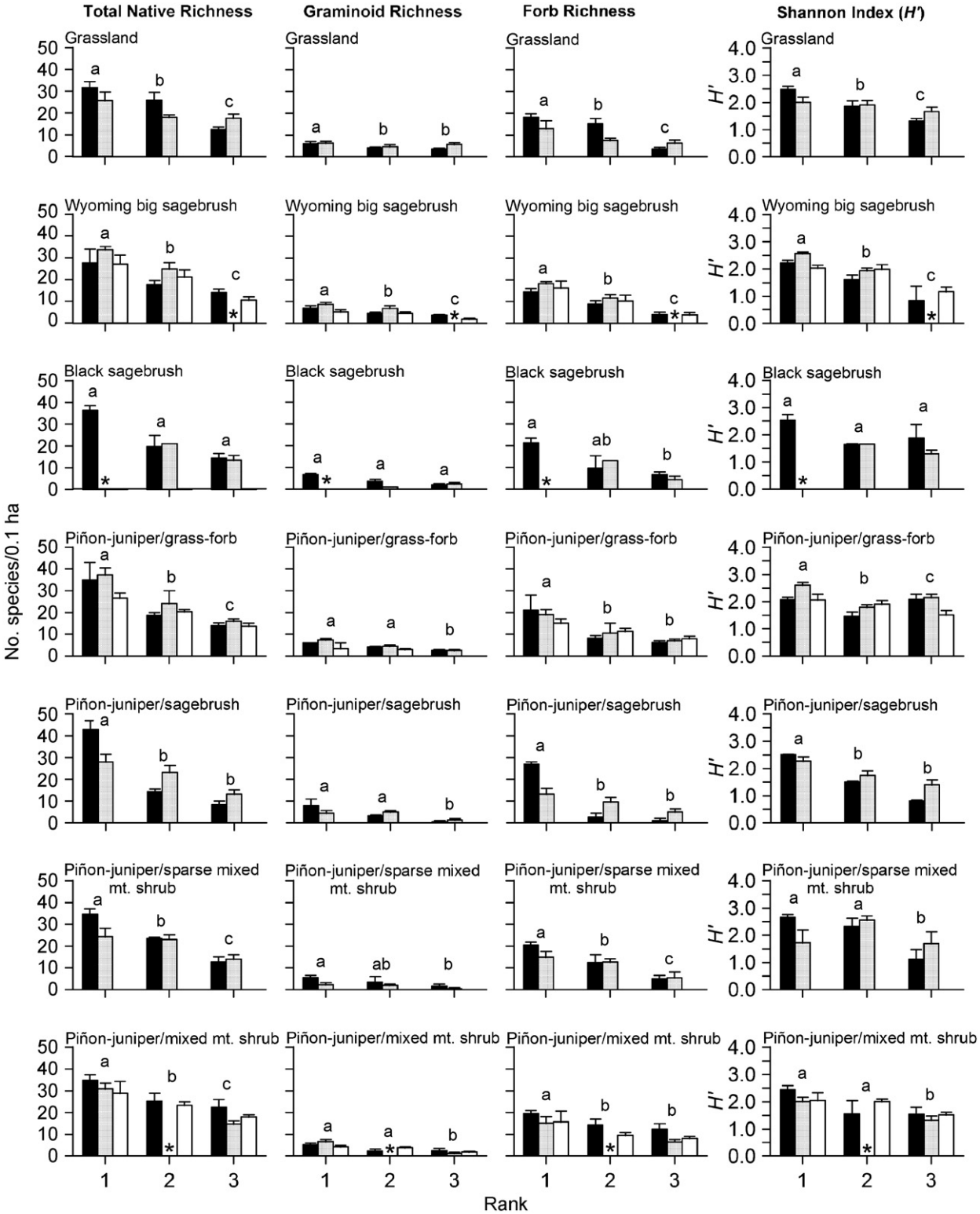


Fig. 3. (*Continued*)

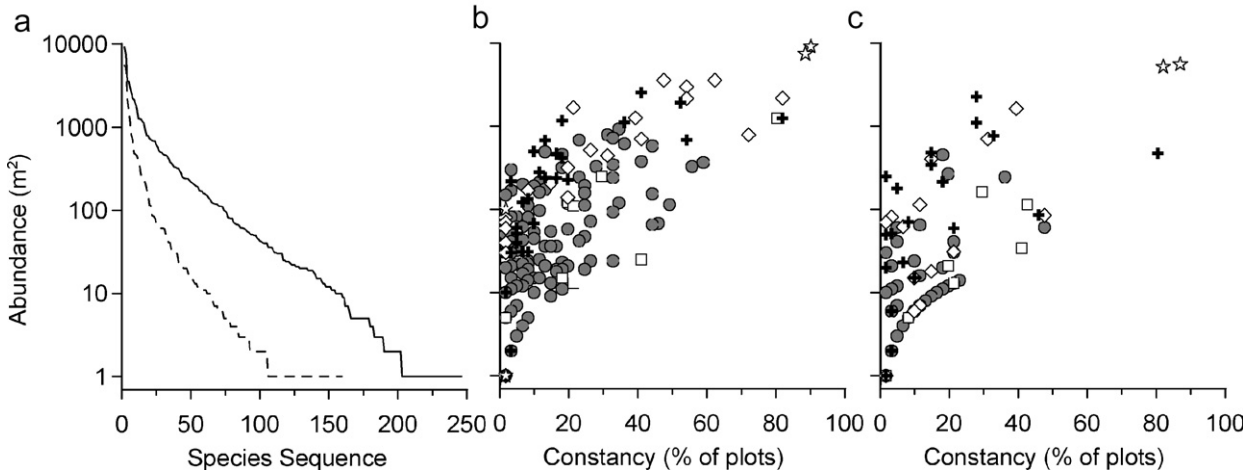


Fig. 4. Native species abundance (total cover area in m^2, logarithmic-scale) vs. species sequence (in rank order from most to least abundant) for Rank 1 sites (solid line) and Rank 3 sites (dashed line) (a) and native species abundance vs. constancy (% occurrence among all plots) for Rank 1 sites (b) and Rank 3 sites (c) $N = 64$ sites for each rank. Symbol shapes represent major species groups as follows: gray circles = forbs, white diamonds = graminoids, white squares = cacti, black crosses = shrubs, and white stars = trees.

Table 4
p-Values, with odds-ratio and direction of rank change within parentheses, for each predictor variable in the ordinal logistic regression model that was used to test for the dependence of ranks on environmental factors

Variables	Black sagebrush (VT3.0)	Piñon–juniper (VT4.4–4.5)	Piñon–juniper (VT4.7–4.8)	Piñon–juniper mixed mountain shrub (VT5.0)
Elevation (m)	–	–	–	–
Slope (deg.)	–	–	0.007 (0.87−)	–
Aspect (cosine transformed)	–	0.036 (0.18−)	0.012 (5.17+)	0.007 (2.77+)
Geologic substrate				
Shale	0.016 (26.35+)	–	–	–
Other	–	–	–	–
Sandstone	–	–	–	–

Environment, slope, and aspect were continuous predictor variables while geologic substrate was a categorical predictor variable. (+) indicates significantly increased odds of a superior reference rank (i.e., 3→1), while (−) indicates significantly increased odds of an inferior rank (i.e., 1→3).

environmental subset was valid. These results suggest that ranks still represent a degradation gradient, even though the OLR models implied that aspect played a role in ranks. Also, although more calcareous sandstone substrates may favor soil crust development (Belnap et al., 2001), the 32 Rank 1 sites restricted to these substrates averaged 28.3% cover, compared to 6.7% cover for the 18 Rank 2 and 3 sites combined ($t = 4.57$, $p < 0.001$, d.f. = 41).

Fig. 3. Mean values among ranks at the community level (a single bar) for (a) percent-cover measures and (b) measures of diversity. Each row of graphs is one of seven major vegetation types, while each column of graphs is a percent-cover or diversity variable. Sets of 2–3 community types in a major vegetation type are represented by 2–3 adjacent bars, and shading of adjacent bars represents the sequential community type codes within each major vegetation type (e.g., black = VT2.1, gray = VT2.2, white = VT2.3). Communities with no sites assigned to a particular rank are indicated by "*". Where no bar is visible, but no "*" is shown, the value is near zero (e.g., 0.1). Error bars represent 1 standard error at the community type level. Mean values at the vegetation-type level that do not differ significantly (using Fisher's tests) among ranks share the same letter (e.g., "a").

4. Discussion

4.1. Reference areas

Comparing extant reference areas to non-reference areas is commonly used in ecological research to test hypotheses about land-use effects on vegetation, to help define ranges of natural variability, and to guide ecological restoration and management (Christensen et al., 1996; White and Walker, 1997). Examples include comparing understory communities in logged vs. old-growth forests (Scheller and Mladenoff, 2002) and soils in grazed vs. ungrazed semi-desert grasslands (Neff et al., 2005). Our approach used relict sites and protected areas as potential reference "markers" in ordination space, allowing assignment of a larger random sample of sites to ranks based on their position along a gradient of degradation (or, conversely, naturalness). The success of this approach was partially evident by the relatively consistent alignment of rank designations *vis-à-vis* the means for community variables tested using Fisher's LSD (Fig. 3). Moreover, comparisons of species abundance and frequency indicate that key species are often absent or poorly represented in degraded sites (Fig. 4), especially native cool-season bunchgrasses, but also numerous forbs (Supplementary material Appendix 2, electronic version).

Although significant differences commonly existed among ranks, indicating degradation, some exceptions occurred. At the vegetation level, the black sagebrush type generally lacked differences among ranks (Fig. 3), due, in part, to small sample sizes and correspondingly high confidence intervals. Variability within each community also resulted in a few questionable ranks. For instance, while most reference sites initially assigned to Rank 2 had more past or seasonal grazing than Rank 1 sites, one site each from the grassland and piñon–juniper/grass–forb vegetation types fell in Rank 2 in the ordination, in spite of being relatively species-rich and in relict areas. This probably occurred because of slightly unusual species composition and cover within those vegetation types, including forb percent cover well below the mean for Rank 1 sites. Similarly, some random sample sites assigned to Rank 1 lacked in either species richness, grass cover, or forb cover compared to other Rank 1 sites, but had modestly higher values for at least some of these variables compared to Rank 2 sites. These few ranking problems did not alter overall trends among ranks within vegetation types (Fig. 3), but underscore the need to manage areas on individual merit rather than rank alone.

4.2. Potential environmental influences on ranks

Although the OLR results indicated that environment was significantly associated with rank in 4 of 7 vegetation types/subtypes (Table 4), this likely reflects the limited spectrum of reference sites that could be found within the heavily utilized study area, rather than a definitive influence over ranks. For instance, both Colorado National Monument and Sewemup Mesa, where piñon–juniper/mixed mountain shrub reference sites were largely found, contain predominantly gently sloping, north- and east-facing mesa tops. For these communities, ranks held even among the subset of sites matching the environment of these reference sites. For black sagebrush, geologic substrate potentially influenced ranks, yet among reference areas it was limited to Morrison substrates and was represented by only three samples, resulting in a very large confidence interval (1.85–374.94) for the odds ratio and limiting inferences regarding the potential influence of geologic substrates. The influence of northeast aspects on poorer ranks in piñon–juniper/sagebrush communities was likely due to environmental limitations outside reference areas, where 75% of sites were on north- and east-facing slopes.

This inability to completely match the environments of reference and non-reference sites was a potential limitation of the approach used here, but is a limitation for all reference-area studies. Unfortunately, remaining reference areas are few, often found in rocky, rugged locations of shallow soil-depth, whereas accessible, naturally productive sites have long been influenced by livestock grazing and other land uses. Nonetheless, land use, rather than environment, was the main influence on rank for 5 of 7 vegetation types/subtypes. For the other two, the black sagebrush and piñon–juniper/sagebrush communities, which collectively represent 33 sites or 11.8% of all analyzed sites, the evidence that environment influenced ranks is inconclusive. Overall, similar compositional trends among ranks for all vegetation types (Fig. 3), including reduction of native bunchgrasses (Supplementary material Appendix 2, electronic version), suggests that the

analysis method does elucidate a gradient in degradation due to land use, consistent with other relict/reference area research, as discussed below.

4.3. Potential land-use influences on ranks

Potential land-use influences on ranks in the study area include fire exclusion, clearing or thinning of overstory trees and shrubs, and livestock grazing. Fire exclusion can alter understory plant species composition, but results vary among vegetation types, environments, and fire characteristics (e.g., seasonality, intensity) (e.g., Evangelista et al., 2004; Wrobleski and Kauffman, 2003). Low-severity surface fires were absent or rare in piñon–juniper woodlands of the Uncompahgre Plateau; instead, stand-replacing fires occurred every 400–600 years (Shinneman, 2006), as in these woodlands elsewhere in southwestern Colorado (Floyd et al., 2004). Fire in black sagebrush and Wyoming big sagebrush is generally stand-replacing, with fire rotations of 100–240 years or more (Baker, 2006). Given long intervals for stand-replacing fire and lack of surface fire, it is unlikely piñon–juniper and sagebrush ecosystems are affected by fire exclusion, but effects on grasslands are less certain.

Overstory treatment (e.g., chaining) may have influenced ranks. Of 239 non-reference sites, 33 were treated; 17 (51.5%) of these fell in Rank 3, 13 (39.4%) in Rank 2, and 3 (9.1%) in Rank 1. Rank 1 treated sites included only lightly thinned piñon–juniper stands, while 60% of Rank 2 and 3 treated sites had mature overstory trees removed. With over half of treated sites falling in the most degraded condition (Rank 3), clearing treatments were not successful at restoring understory communities.

The most ubiquitous and significant land-use influence on communities in the study area outside most reference areas is livestock grazing. Although the analysis does not represent a controlled experiment that allows direct analysis of the effects of different grazing animals, grazing intensity, or grazing systems, it does essentially reflect the contribution of livestock grazing since EuroAmerican settlement to ecosystem degradation and change. Moreover, these results have not been skewed by spatially disproportionate effects of native herbivores, as all reference areas and other sites are accessible to native animals. Below, key community differences among reference ranks are discussed, with a focus on the potential influence of livestock grazing.

4.4. Herbaceous and biological soil crust cover are greater in reference than non-reference areas

Mean native graminoid percent cover was significantly greater in Rank 1 than either Rank 2 or 3 sites, or both, among all vegetation types, especially for cool-season grasses, and was as high as 50–80% for some reference area communities (Fig. 3a). Similarly, *Poa fendleriana* was documented as high as 80% cover in nearby Mesa Verde, Colorado, where grazing has been excluded since the early 1930s (Floyd and Colyer, 2003). Native, cool-season bunchgrasses, especially *P. fendleriana*, *L. salinus*, *A. hymenoides*, and *H. comata*, were also the most under-represented grasses on degraded sites in this study (Supplementary material Appendix 2, electronic version), consistent with research elsewhere in the Intermountain West. For example, the dominant cool-season bunchgrasses, *P. fendleriana* and *H. comata*, were twice as abundant on a near-relict piñon–juniper/sagebrush site in Utah compared to a grazed site, though overall grass cover was not significantly different (Guenther et al., 2004). *H. comata* was far more abundant in relict sagebrush communities than surrounding grazed landscapes in Utah (Madany and West, 1984), and *P. fendleriana* dominated the sparse grass cover on an Arizona relict, but was replaced by *B. gracilis* on surrounding grazed landscapes (Jameson et al., 1962). In Chaco Culture National Historic Park, New Mexico, where livestock grazing was removed from most areas by 1948, cool-season bunchgrasses dominated, while grazed sites outside the park were dominated by warm-season grasses with generally less percent cover (Floyd et al., 2003). Similar findings have been reported for grazing exclosures in sagebrush communities (e.g., Anderson and Inouye, 2001). These differences in native graminoid composition and abundance are likely due to greater grazing resistance of many warm-season and rhizomatous grasses relative to most cool-season bunchgrasses (Mack and Thompson, 1982; Milchunas et al., 1988).

Mean forb cover was higher in Rank 1 than in Ranks 2 and 3 sites, among all vegetation types, and significantly so in most vegetation types. Forb cover has not been well documented in reference area research

in semi-arid ecosystems of the Intermountain West. However, Guenther et al. (2004) and Schmutz et al. (1967) found little difference in forb cover between grazed sites and ungrazed relict sites. Among grazing exclosure studies, findings have varied. For instance, Anderson and Inouye (2001) found a three-fold increase in the density of forbs 40 years after livestock grazing removal. However, forb cover can be higher on grazed piñon–juniper landscapes vs. ungrazed relicts (Harris et al., 2003), and livestock grazing may increase or decrease native forbs depending on factors such as soil types (Gelbard and Harrison, 2003) and climate (Vesk and Westoby, 2001). Significant loss of forb cover and diversity found in this study may in part reflect the environment of the study area, but more likely reflects the long term or complete absence of livestock in most reference areas, a larger sample size than most studies, and more degraded conditions in sites outside reference areas.

Significantly higher mean biological soil crust cover in Rank 1 sites among most vegetation types (Fig. 3a) mirrors other reference area research in the Intermountain West (Beymer and Klopatek, 1992; Kleiner, 1983). Guenther et al. (2004) found 27% and 60% greater cover for overall biological soil crust and well-developed, older soil crust, respectively, on a piñon–juniper/sagebrush relict site in Utah compared to a grazed site. Floyd et al. (2003) found that nitrogen-fixing black soil crust cover was significantly higher on New Mexico grasslands in exclosures ($n = 6$) compared to grazed sites. Anderson et al. (1982) documented soil crust cover increased from 4% to 15% within 14–18 years after grazing exclusion in *Atriplex* shrub communities in Utah.

4.5. Reference areas and degraded areas are similarly at risk for non-native species invasions

Consistent trends among ranks were absent for mean non-native species cover, and a few Rank 1 sites among vegetation types (e.g., piñon–juniper/sagebrush communities) had significantly higher mean cover of non-natives than did sites in Ranks 2 and 3 (Fig. 3a). Some relict-area studies in the Intermountain West found either absence or low abundance of non-native species (Jameson et al., 1962; Madany and West, 1984; Mason et al., 1967). Floyd et al. (2003) found the proportion of non-native species did not vary significantly between grazed and excluded sites in semi-arid grasslands. However, Anderson and Inouye (2001) found the abundance of non-native species increased slightly in sagebrush communities after livestock grazing removal. The relationship between non-native species and livestock grazing is complex, varying with factors such as grazing intensity, and the interactive influence of roads, fire history, nutrient availability, and soil types (Gelbard and Belnap, 2003; Gelbard and Harrison, 2003; Stohlgren et al., 2001).

4.6. Reference areas generally support greater species richness and diversity

One of the more consistent trends was the significantly higher mean for total native species richness and forb species richness in Rank 1 vs. Rank 2 and 3 sites. Indeed, total species richness declined by 80% between Rank 1 and 3 sites in piñon–juniper/Wyoming big sagebrush (Fig. 3b). Mean graminoid species richness was also strongly higher in Rank 1 sites, but not as often significantly different from both Rank 2 and 3 sites (Fig. 3b). Only a few relict-area studies included species richness. Guenther et al. (2004) found no significant differences in richness between grazed and near-relict ungrazed piñon–juniper/sagebrush sites in Utah, but a significant difference in total richness between all ungrazed sites vs. grazed sites. Among livestock exclosure studies, results were variable. Species richness increased after grazing removal in semi-arid grasslands in Arizona (Brady et al., 1989), and shrub, forb, and perennial grass richness increased after grazing exclusion in sagebrush in Idaho, though overall richness did not increase (Anderson and Inouye, 2001). Floyd et al. (2003) found greater species richness in all 6 exclosure sites relative to grazed sites in semi-arid grasslands in New Mexico. Gelbard and Harrison (2003) found that forb species richness increased on non-serpentine soils in California as distance from roads increased and grazing pressure decreased.

Consistent and usually significantly higher mean Shannon diversity was found in Rank 1 sites (Fig. 3b), with few exceptions, suggesting that most reference areas have more species at relatively equal proportions compared to non-reference areas. Few studies measured effects of grazing using diversity indices besides richness. In semi-arid and sub-humid grasslands of the Great Plains, which evolved with native ungulate grazers such as bison, most grazing practices increased species evenness (Hart, 2001; Hickman et al., 2004). However, the semi-arid landscapes of southwestern Colorado likely lacked an evolutionary history of herds of

large grazing herbivores (Paulson and Baker, 2006), and livestock grazing in this area increases dominance by a relatively few plant species probably most tolerant of grazing.

The lognormal vs. log series species abundance curves for Rank 1 and Rank 3 sites (Fig. 4a) also demonstrate a fundamental difference between reference and degraded sites at the landscape level. These distributions indicate a 55% increase in the total number of species for Rank 1 over Rank 3 sites. Equally important, a log series distribution for Rank 3 suggests a larger relative proportion of the biota is uncommon on degraded sites. The log series distribution at the metacommunity level suggests local extirpation and stochastic dispersal processes are more likely for Rank 3 than Rank 1 sites (Ulrich and Ollik, 2004), and populations on Rank 3 sites may be prone to higher rates of local extinctions (Magurran, 2005). In contrast, the log-normal species abundance curve for Rank 1 sites reflects a metacommunity in which a larger proportion of the plant biota is relatively abundant and, hence, is more likely to maintain species composition through low local extinction rates and stable dispersal rates. Also, Fig. 4b and c demonstrate that rates of constancy and cover were higher for most herbaceous species, and constancy was higher for shrub species, in Rank 1 vs. 3 sites. Still, the regional reference landscape exhibits a high degree of spatially stochastic diversity, as 85% of 114 species found in Rank 1, but not Rank 3 sites, occurred in $<5\%$ of these Rank 1 sites. Past livestock grazing may have exacerbated this condition, significantly reducing both population sizes (i.e., cover) and number of populations (i.e., constancy), particularly of native forbs and graminoids (Fig. 4b and c).

4.7. Implications for other ecosystem components, processes, and ecological restoration

The findings demonstrate that the semi-arid grassland, shrubland, and woodland ecosystems of the Uncompahgre Plateau have experienced significant declines in grass and forb cover, biological soil crust cover, native species richness, compositional evenness, and relative species abundance, occurring at both stand- and landscape-levels. Declines in native species diversity and relative abundance can have detrimental consequences for ecosystem productivity, stability, and resilience (Johnson et al., 1996; Tilman et al., 1996), including further biodiversity loss. For instance, native bunchgrasses, which have declined in the study area, form horizontal patterns consisting of interspace gaps between tall individual grasses, a structural habitat component required by the imperiled sage grouse (Sveum et al., 1998). Decline in plant species in the study area likely triggers undocumented declines in richness and diversity among closely-associated non-plant species, including, for instance, insect species that use particular plants as hosts (Thomas et al., 2004). Biological soil crusts function to stabilize soils, fix carbon and nitrogen, increase water retention, and benefit the germination of many native plants (Belnap et al., 2001). Loss of these biophysical surfaces can lead to increased non-native species invasions (Stohlgren et al., 2001), greater wind erosion of soils, and reduced soil fertility, even decades after grazing removal (Neff et al., 2005). Replacement of cool-season bunchgrasses by non-native cheatgrass (*B. tectorum*) can lead to further declines in biological soil crusts and native species through dramatic increases in fire (Belnap et al., 2001; Brooks et al., 2004). It thus seems appropriate to restore the semi-arid ecosystems of the Uncompahgre Plateau to meet sustainable land management and biodiversity conservation goals.

Restoration on the Uncompahgre Plateau will require combinations of active and passive approaches, at both stand- and landscape-levels. Passive ecological restoration typically focuses on reducing adverse effects of land-use practices causing ecosystem degradation, while active restoration employs direct repair of altered ecosystem components and processes (Hemstrom et al., 2002; Whisenant, 1999). For most of the study area, including most Rank 2 and many Rank 3 sites, landscape-level passive restoration may be most efficient, cost-effective, and successful, given the size of the region makes numerous, localized treatments cost-prohibitive. Moreover, native vegetation is relatively unfragmented by development, permitting unimpeded, broad-scale restoration procedures.

Hobbs and Norton (1996) suggest that it is critical to identify the processes that led to degradation, develop methods to ameliorate the degradation, and set realistic goals for restoration within ecological, socio-economic, and cultural limits. Because livestock grazing is the major stressor within the study area and causes similar patterns of degradation among different semi-arid communities (Fig. 3), its removal would expedite ecological recovery across much of the region, as evidenced by livestock removal elsewhere in semi-arid ecosystems of the Intermountain West (Anderson and Inouye, 2001; Brady et al., 1989; Floyd et al., 2003).

However, due to cultural and socioeconomic factors, removing livestock grazing may only be feasible for specific locations within the study area, such as highly sensitive communities or severely degraded sites. Still, there are broad-scale, passive restoration strategies short of complete livestock removal that can be applied, including reducing grazing, using seasonal closures (Weltz et al., 2003), and employing innovative grazing strategies, such as grassbanks (Jensen, 2001).

Regional restoration of native plants will also require protecting extant reference areas as sources of native seed dispersal onto surrounding landscapes (Honnay et al., 2002), and this strategy should include periodically monitoring these areas for ecological threats, such as invasive species or heavy human use. Indicator species can also be regularly monitored to measure passive restoration success (White and Walker, 1997). Large grazing exclosures are warranted in currently unrepresented environments across the region to complete the representation of vegetation in reference areas.

The most highly degraded Rank 3 sites, that have little or no herbaceous or biological soil crust cover, and for which overgrazing is a cause, may require intensive active restoration at local scales, including reseeding, soil stabilization, and eradication of detrimental non-native species, to restore autogenic ecosystem processes (Hemstrom et al., 2002; Whisenant, 1999). Determining which areas warrant active restoration and their specific needs may require a two-pronged approach: first, by determining the degree and effects of overgrazing using rangeland health indicators (Breckenridge et al., 1995) and, second, by using a "scorecard" for key community components, such as bunchgrass cover, that allows explicit comparisons of current conditions to estimates of ranges of natural variability (e.g., a range of percent cover) for each component (Caraher and Knapp, 1995; Hobbs and Norton, 1996). To avoid further damage to sensitive biological components, including soil crusts, low-impact planting techniques may be used, such as aerial applications. Moreover, native seed mixes can be collected from nearby reference areas to maintain the integrity of local plant community diversity (Kaye, 2001). Seeding programs that uniformly apply a "native" plant seed-mix over large areas are ecologically inappropriate, as this may irrevocably alter native plant community beta diversity, including spatially variable genetic diversity, highly unique local floras, and rare species (Kaye, 2001), which have been documented on the Uncompahgre Plateau (Lyon and Williams, 1998). Herbaceous diversity in Rank 1 sites includes numerous species with low abundance and constancy among sites (Fig. 4b), suggesting highly stochastic patterns of plant diversity and considerable vulnerability of a large component of the native flora in the study area.

In summary, both active and passive approaches will be required to restore native plant communities on the Uncompahgre Plateau. However, widespread changes in livestock grazing practices are the most effective means to achieve restoration across this large land area, even if achieved gradually. As ecological considerations continue to influence management on public lands, a critical near-term strategy would focus on protection of extant reference areas, combined with an ambitious program to establish a strategically located network of new reference areas. Not only do reference areas have inherent biological conservation value, but they will also provide benefits to future restoration efforts, as sources of scientific information and native species dispersal.

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Appendix A. Supplementary data

The online version of this article contains additional supplementary data. Please visit doi:10.1016/j.jaridenv.2007.06.002.

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