



Comparison of species and trait-based approaches for describing sagebrush steppe response to range management

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Chemical shrub treatment; Community dynamics; Ecological site; Functional groups; Grazing; Monitoring; Northwestern Colorado; State-and-transition models

Nomenclature

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Abstract

Question: Is valuable information lost when plant trait group composition is used, rather than species composition, to describe plant community response to range management?

Location: Elkhead Watershed, Colorado, US.

Methods: Current model-building efforts use species composition to define changes in ecosystem state, but plant traits may offer a faster and more broadly applicable alternative. We (1) compare states defined by species composition to those defined by trait-based groups of differing complexity and (2) determine how management and environmental site characteristics relate to species- and trait group-defined states. We sampled 72 plots with different grazing and chemical shrub treatment histories on two soil types. We measured plant species composition in each plot and categorized species into trait groups using three classification schemes, which represented increasing numbers of traits and levels of classification complexity. The classifications employed easily measured traits that affect plant response to range management: life form, life history, resprouting ability, height, vegetative reproduction and N-fixation. Using hierarchical cluster analysis, we identified states with similar species or trait group composition. We explored relationships between each set of potential states and management history and environmental factors using logistic regression.

Results: Trait-based group composition and species composition identified many of the same potential states and responses to grazing and chemical shrub treatment. Relationships between species and trait group composition and management and environmental characteristics differed on the two soil types. Species composition was sensitive to more different management practices, on average, than trait group composition. Trait group composition revealed some relationships to management and environmental drivers that were not detected using species composition.

Conclusion: This study confirms that species composition is a more sensitive indicator of sagebrush steppe response to range management, and some information is lost with a trait-based approach. However, traits also add to depth of understanding by revealing additional community patterns related to different drivers. Using the most complex trait grouping scheme that is feasible in a particular study, and also looking for patterns based on simpler trait groups, will provide the most complete understanding of sagebrush steppe response to range management.

Introduction

Understanding plant community responses to land management is crucial because plant communities can alter

ecosystem function (Chapin et al. 1997) and the provisioning of ecosystem services (Havstad et al. 2007). However, the time involved in studying individual species' responses and the complexity of scaling responses up to

the community or region necessitate alternative approaches (Suding et al. 2008). One promising way to understand community response to management is through groups of plant species with similar traits (hereafter, trait groups; TGs). A growing literature links land management to changes in abundance of plant traits at the community level. Whereas changes in species abundances are localized to the area where that species occurs, many changes in TG composition are generalizable across different sites and regions (Diaz et al. 2004; Bond et al. 2005; Cornwell et al. 2008). For example, a global analysis of trait responses to grazing showed that heavier grazing favours short, prostrate and annual plants vs tall, erect or perennial plants (Diaz et al. 2007). For this reason, TGs are commonly used to understand and predict how ecosystems will respond to management in ecosystem monitoring (de Bello et al. 2010) and modelling efforts (Bond et al. 2005; Euskirchen et al. 2009). In this paper, we compare plant species and trait-based group composition as indicators of plant community response to range management in sagebrush steppe of the western US.

Globally, numerous efforts are underway to develop state-and-transition models (STMs) to assist with land management decision-making (Bestelmeyer et al. 2009; Hobbs & Suding 2009). These conceptual models describe plant community change in response to disturbance as a set of shifts between alternate states. Differences in species composition are often used to identify states in STMs (e.g. Allen-Diaz & Bartolome 1998), under the assumption that changes in species correspond to changes in underlying processes maintaining states. This approach requires careful sample stratification by land units with uniform soils and climate, called *ecological sites* in the US (USDA NRCS 2003). However, trait-based methods may be a useful alternative to species-based methods for identifying alternate states because they provide mechanistic links to management practices and positive feedbacks (Gondard et al. 2003; Quetier et al. 2007) and reveal generalizations across regions (Diaz et al. 2004; Bond et al. 2005; Cornwell et al. 2008). Indeed, many sagebrush steppe studies have shown coordinated TG responses to management: for example, shrub removal increases cover and production of herbaceous plants by reducing competition (Mueggler & Blaisdell 1958; Eckert et al. 1972; Harniss & Murray 1973). In addition, simpler trait-based approaches may expedite the STM building process and create models that are more easily accessible to land managers.

Although many TGs are identified using a data-driven approach, *a priori* approaches have been more commonly applied in the sagebrush steppe. The data-driven approach employs quantitative measures of traits to identify 'clusters' of plant species with similar traits using multivariate statistics (e.g. Lavorel et al. 1997; McIntyre et al. 1999;

Diaz et al. 2004). Data-driven studies have found that life form (grass, forb, shrub) is related to many other plant traits (e.g. Westoby & Leishman 1997), and therefore recommend a hierarchical approach to TG classification based on life form (Lavorel et al. 1997). Life form has been found to be related to disturbance in previous studies of the sagebrush steppe (Blaisdell 1953; Mueggler & Blaisdell 1958; Harniss & Murray 1973). Most TG classifications used in sagebrush steppe have followed this recommendation, with grass, forb and shrub groupings further subdivided by photosynthetic pathway (Derner et al. 2008), annual vs perennial life histories (Pellant et al. 2005; Bates et al. 2006; Derner et al. 2008), N-fixation (Pellant et al. 2005; Goergen & Chambers 2009), growth form (e.g. bunch vs rhizomatous; Pellant et al. 2005), re-sprouting vs not (Riegel et al. 2006) and height differences (Pellant et al. 2005; Bates et al. 2006). These TGs respond differently to changes in precipitation (Bates et al. 2006; Derner et al. 2008), burning (Blaisdell 1953; Mueggler & Blaisdell 1958) and chemical shrub treatment (Mueggler & Blaisdell 1958; Harniss & Murray 1973). They also affect functional attributes such as ecosystem resistance to invasion (Davies 2008) and carbon cycling (Knapp et al. 2008).

This study compares plant species and trait group composition as indicators of ecosystem response to range management in the sagebrush steppe. We sampled plant cover by species in 72 plots representing two ecological sites and a variety of management histories to infer the effects of management on the abundance of plant species and TGs. These two ecological sites represent two highly contrasting soils and plant communities that are common throughout the sagebrush steppe: Claypan is characterized by heavy clay soils dominated by alkali sagebrush, whereas Mountain Loam has loamy soils, an overstorey of mountain big sagebrush with resprouting shrubs, and a more productive and diverse understorey. Three TG classification schemes were defined *a priori*, drawing on previous studies of response to management in sagebrush steppe. In order of ascending complexity, they are: Simple, Practical (chosen to be identified quickly in the field) and Complex (Fig. 1).

Trait-Based			
Group	Grasses	Forbs	Shrubs
Simple	Annual vs. Perennial	Perennial	
Practical	Short vs. Medium vs. Tall	Short vs. Medium vs. Tall	Resprouting vs. Non
Complex	Vegetative Reproduction vs. None	Vegetative Reproduction vs. None, N-Fixing vs. Not	Resprouting vs. Non
Species			

Fig. 1. Traits used to identify trait group composition and define potential alternate states in the sagebrush steppe, northwestern Colorado, USA. Trait groups increase in complexity from Simple groups based on growth form and life history to Species.

First, we compare potential alternate states based on TG composition with potential states based on species composition and ask: *do the two approaches identify the same overall vegetation patterns?* Next, we explore how potential alternate states based on TG composition are related to site management history and environmental variation, two important drivers of vegetation pattern in the study area (Kachergis et al. 2012). Given our purpose, the indicator that provides the most information would define states that are most related to both range management practices and variation in sites' environmental characteristics. This study has important implications for choosing plant species composition vs TG composition in building STMs and designing monitoring studies to understand plant community response to management.

Methods

Study area and site selection

This study was conducted on private and public rangelands in and near the Elkhead Watershed of northwestern Colorado, US. Fifteen private landowners, the Bureau of Land Management (BLM) and the US Forest Service (USFS) participated and shared management history (Knapp 2008). Sampling focused on the Claypan and Mountain Loam ecological sites, defined as two different types of land with characteristic soils, climate and vegetation (USDA NRCS 2003). Areas that represent all existing combinations of management practices were identified: historic grazing intensity, a qualitative estimate of typical stocking rate based on interviews with 26 local land managers (Knapp 2008); and shrub management practices, including chemical treatment (aerial spraying with herbicide), mechanical treatment or none. Plot locations were stratified first by ecological site, then by management history, and randomly located at least 200 m apart.

Detailed methods are reported in Kachergis et al. (2011), but they are summarized here. We sampled seventy-six 20 × 50 m plots for vegetation in 2007 and 2008 and for soils in 2009.

Soil and environmental data collection

Soil data were collected to verify the ecological site and to determine whether plant species and TG composition were related to environmental variation. Each horizon was described to 50 cm according to NRCS protocols (Schoeneberger et al. 1998) using a pit or augur hole in the centre of each plot. The ecological site for each plot was verified by matching soil descriptions with the Claypan and Mountain Loam ecological site soil descriptions (USDA SCS 1975). Claypan is characterized by a thin clay loam or clay surface horizon over a clay subsoil that restricts water

movement and availability, while Mountain Loam is characterized by a thicker loam or clay loam surface horizon and a clay loam or clay subsurface. We sampled 33 Mountain Loam and 39 Claypan plots. Percentage clay in the top 10 cm was calculated as a weighted average of hand texture by horizon and horizon thickness. We also recorded slope and aspect for each site to determine whether plant species and TG composition were related to environmental variation, another important driver of vegetation pattern in the study area (Kachergis et al. 2012).

Plant species and trait group composition

We measured plant foliar cover by species using the line-point intercept method, sampling at 1 m intervals along five 50-m transects spaced 5 m apart in the plot (250 points per plot; Bonham 1989). Trait group composition was calculated from species composition by adding all species' foliar cover in each trait group. Traits for each species were identified using species descriptions from the USDA PLANTS database 'Characteristics' sheets (USDA 2010), supplemented by XID (height and rhizomatous/stoloniferous growth form; Flora ID Northwest 2009) and the Fire Effects Information System (resprouting capability of shrubs; USFS 2010). Traits were chosen to use in the classifications based on their relationship to major management practices and ease of use in monitoring: plant height (Short <40.6 cm, Medium 40.6–121.9 cm, Tall >121.9 cm), presence or absence of rhizomes and annual/perennial life history are related to grazing, and life form and whether shrubs are re-sprouting or not are related to chemical shrub treatment. Species were categorized into TGs at three different hierarchical levels of complexity within life form (Fig. 1).

Data analysis

We compared potential states based on TG composition with potential states based on species composition to determine whether the two approaches identified the same overall vegetation patterns. We used agglomerative hierarchical cluster analysis to identify potential states based on similarity in species and TG composition, meaning foliar cover of species and TGs (Bray–Curtis distance measure, Flexible β linkage method with $\beta = -0.25$). The cluster dendrograms were pruned quantitatively based on indicator species analysis (ISA), which generates an indicator value of 1–100 based on each species' faithfulness and exclusivity to that group (Dufrene & Legendre 1997). Dendrograms were pruned at the number of groups with the lowest average P -value for all species based on a randomization test (1000 randomizations), interpreted as the most ecologically meaningful number of groups (McCune

& Grace 2002), up to a maximum of seven groups. We compared species composition and trait group composition among potential states, thus confirming the validity of the clusters, using pair-wise multi-response permutation procedure (MRPP) on Bray–Curtis distance. MRPP tested the hypothesis of no differences among groups of plots (McCune & Grace 2002). This non-parametric method compared the observed weighted mean within group distance in a distance matrix to the distance that would be expected by chance. This test produced a *P*-value and a measure of effect size called the chance-corrected within-group agreement (*A*), which ranged from 0 (no effect) to 1. We used an α of 0.05, and ecologically significant differences are often found when *A* is <0.1 (McCune & Grace 2002). MRPP confirmed that the clusters were significantly different in species and trait composition, with *P* < 0.0001 for all tests and *A* ranging from 0.18 (Mountain Loam Species) to 0.49 (Claypan Simple). Cluster analysis, ISA and MRPP were performed using PC-ORD (v. 5.0, MjM Software Design, Gleneden Beach, OR, US).

To identify how potential states based on TG composition are related to rangeland management and environmental variation, we used logistic regression in SAS (v. 9.2, SAS Institute 2002–2008, Cary, NC, US), with site history and environmental variables as predictors of state membership. Site history variables were chemical shrub treatment (categorical: sprayed vs not; 11 vs 28 plots in Claypan and 7 vs 26 plots in Mountain Loam) and historic grazing intensity (ordinal: below medium vs medium high vs high; Claypan: 13, 13 and 7 plots; Mountain Loam 15, 7 and 16 plots). Environmental variables (all continuous) were percentage clay in the top 10 cm, slope and aspect. Aspect was transformed into a continuous variable, with higher values for more productive north-eastern slopes (Beers et al. 1966). Significance was assessed at *P* < 0.10 to ensure that all meaningful variables remained in the model and given our relatively small sample size. Before analysis, we tested for and failed to find any correlations among predictor variables.

Results

Comparison of species- and trait group-defined states

Several Mountain Loam and Claypan potential states defined by Complex TGs are similar to species-defined states (Tables 1 and 2; Appendices S1 and S2). We define states as similar when indicator species of the species-defined potential state correspond to the indicator trait group of the TG-defined potential state and when states contain over 50% of the same plots, although the reader may judge for themselves (Tables 1 and 2). For example, Mountain Loam CO1 and PR1 are characterized by

Table 1. Relationships among site management history, environmental variables and potential states for the Mountain Loam ecological site. States are based on species composition and Complex, Practical and Simple trait-based group composition, with number of plots in each state in parentheses. Relationships are significant according to logistic regression at *P* < 0.10; italics indicate qualitative analysis (e.g. All with chemical shrub treatment). Grey shading indicates potential states that are 50% similar to each other, and the Overlap column shows percentage of plots shared between similar states (shared plots/total plots in larger state).

Species	Complex			Practical			Simple		
	State (M)	Site mgmt. history/enviro.	Overlap (%)	State (M)	Site mgmt. history/enviro.	Overlap (%)	State (W)	Site mgmt. history/enviro.	Overlap (%)
SP1 (5)	Grazing intensity (+)	100	CO1 (5)	Grazing intensity (+)	100	PR1 (5)	Grazing intensity (+)	S11 (8)	Slope (+)
	Slope (-)			Slope (-)			Slope (-)		Clay (-)
SP2 (12)	Clay (+)	50	CO2 (7)	Clay (+)		PR2 (11)	Grazing intensity (-)	S12 (3)	-
	Slope (-)			Slope (+)			Slope (+)		-
SP3 (5)	Clay (-)	60	CO3 (4)	Slope (+)		PR3 (5)	-	S13 (15)	-
	Slope (+)			Grazing intensity (-)			Clay (+)	S14 (4)	-
SP4 (7)	Chemical shrub treatment (+)	50	CO4 (8)	Grazing intensity (-)		PR4 (10)	Clay (+)	S15 (2)	-
	-		CO5 (7)	-		PR5 (1)	Burned 2 yr ago	S16 (1)	Burned 2 yr ago
SP5 (4)	-		CO6 (1)	Burned 2 yr ago		PR6 (1)	Burned 2 yr ago		
			CO7 (1)	Burned 2 yr ago					

Table 2. Relationships among site management history, environmental variables and potential states for the Claypan ecological site. States are based on species composition and Complex, Practical and Simple trait-based group composition, with number of plots in each state in parentheses. Relationships are significant according to logistic regression at $P < 0.10$; italics indicate qualitative analysis (e.g. All with chemical shrub treatment). Grey shading indicates potential states that are 50% similar to each other, and the Overlap column shows percentage of plots shared between similar states (shared plots/total plots in larger state).

Species	Complex		Practical		Simple	
	State (N)	Overlap (%)	State (N)	Overlap (%)	State (M)	Overlap (%)
SP1 (10)	CO1 (6)	60	PR1 (9)	56	S11 (12)	75
	Site mgmt. history/enviro.		Site mgmt. history/enviro.		Site mgmt. history/enviro.	
	Chemical shrub treatment (+)	All with chemical shrub treatment	Chemical shrub treatment (+)			
SP2 (6)	CO2 (9)	67	PR2 (6)	67	S12 (3)	50
	Slope (+)	Slope (+)				Distance from water (-)
	Clay (-)	Clay (-)				
SP3 (7)	CO3 (9)	67	PR3 (9)		S13 (9)	
	Transformed aspect (-)		Grazing intensity (-)			
SP4 (4)	CO4 (2)	50	PR4 (6)		S14 (4)	
						Chemical shrub treatment (+)
SP5 (3)	CO5 (8)		PR5 (3)		S15 (5)	
						Transformed aspect (-)
SP6 (5)	CO6 (1)		PR6 (4)		S16 (5)	
						Slope (-)
SP7 (4)	CO7 (4)		PR7 (2)		S17 (1)	
	Transformed aspect (+)	Transformed aspect (+)				

non-resprouting shrubs and contain the same plots as SP1, which is characterized by the non-resprouting shrub *Artemisia tridentata* subsp. *vaseyana* (Appendix S1). On Claypan only, some Simple TG-defined potential states are over 50% similar to species-defined potential states (Appendix S2). Both SP1 and SP2 have analogues in all TG classification schemes, with shrubs and grasses as indicator TGs, respectively. Despite many similarities, there are also many TG-defined potential states that differ from species-defined states on both soil types.

Management and environment predict species- and trait group-defined state membership

For both Mountain Loam and Claypan ecological sites, most Species, Complex and Practical potential states were related to site history and/or environmental variation (Tables 1 and 2). Simple TG-defined potential states were generally not related to management or environmental variation on Mountain Loam, but they were on Claypan. TG-defined potential states that were similar to species-defined states generally had the same relationships to management and environmental variation, whereas TG-defined states that were not similar either revealed new relationships or were not related to management or environmental variation (Tables 1 and 2).

Sensitivity to management practices differed among the trait grouping schemes, as shown by the fact that management practices differ in their relationships to potential states defined using each (Table 3). Historic grazing intensity is more closely related to TG composition than species composition in Mountain Loam, but is only related to one Practical state in Claypan. Chemical shrub treatment is more related to species composition than TG composition in Mountain Loam, but species and TGs are equally related to chemical shrub treatment in Claypan (Photos S1, S2). Overall, number of management practices related to potential states increased with complexity of the trait group scheme in Mountain Loam, but remained high even with Simple TGs in Claypan (Table 3).

Sensitivity to environmental variation was similar among trait grouping schemes (Table 3), with states related to at least two of the three environmental variables in each, except Claypan Practical.

Discussion

Species- and trait-based approaches identify many of the same patterns in plant community composition

The *a priori* trait grouping schemes examined in this study are hierarchical: each TG is a combination of more complex TGs (Fig. 1). We found that species and TG

Table 3. Sensitivity of each trait grouping scheme to different management and environmental variables. Significance tests (NS or lowest *P*-value) indicate whether or not there was a significant relationship between a management practice or environmental variable and a state in that trait grouping scheme according to logistic regression. Potential states were defined by Simple, Practical and Complex trait groupings and species composition.

	Simple		Practical		Complex		Species	
	ML	CP	ML	CP	ML	CP	ML	CP
Management								
Grazing intensity	NS	NS	0.01	0.08	0.05	NS	0.08	NS
Distance from water (proxy for grazing intensity)	NS	0.09	NS	NS	NS	NS	NS	NS
Chemical shrub treatment	NS	0.05	NS	0.01	NS	All	<0.01	<0.001
<i>Sensitivity</i> (no. management factors associated with a state)	0	2	1	2	1	1	2	1
<i>Average sensitivity</i>		1		1.5		1		1.5
Environment								
Clay	0.05	NS	0.05	NS	0.05	0.01	0.01	0.03
Slope	0.04	0.02	0.04	NS	0.03	0.05	0.04	0.07
Aspect	NS	0.08	NS	NS	NS	0.03	NS	0.04
<i>Sensitivity</i> (no. environmental factors associated with a state)	2	2	2	0	2	3	2	3
<i>Average sensitivity</i>		2		1		2.5		2.5

approaches identified many of the same patterns in plant community composition (Tables 1 and 2; Appendices 1 and 2), especially more complex TGs. This supports previous research that has found agreement in vegetation patterns identified using species- and TG-based approaches with multivariate methods (Webb et al. 1970; Werger & Sprangers 1982). A mechanism for the agreement is that dominant species often have unique traits and thus compose a majority of their TGs (Walker et al. 1999), driving some similarities between states defined by species and TG composition. For example, several species of *Artemisia* (sagebrush) are the primary non-resprouting shrubs on these soil types, and non-resprouting shrubs are indicators of TG-defined states that correspond to sagebrush-dominated potential states on both soil types (Fig. 2). Likewise, *Pascopyrum smithii* (western wheatgrass) is the dominant medium-height clonal grass in the area, and a species- and a complex TG-defined state are characterized by this grass on both soil types (Fig. 2).

Simple TGs captured similar vegetation patterns as species on Claypan but not Mountain Loam. This occurred when a single Simple TG dominated potential states, corresponding to multiple species. For example, states were identified in all three TG classifications that are similar to Claypan SP1, a native grassland, even though SP1 is not characterized by one dominant species but by a dominant TG (perennial grasses) that corresponds with species patterns. The difference in the overlap between Species and Simple TGs on the two soil types is likely related to the higher species and TG diversity of Mountain Loam relative to Claypan, and suggests that Simple trait groups may not be as useful on soil types with more diverse plant communities.

In contrast, some species-defined states did not correspond to TG-defined states. These states had many

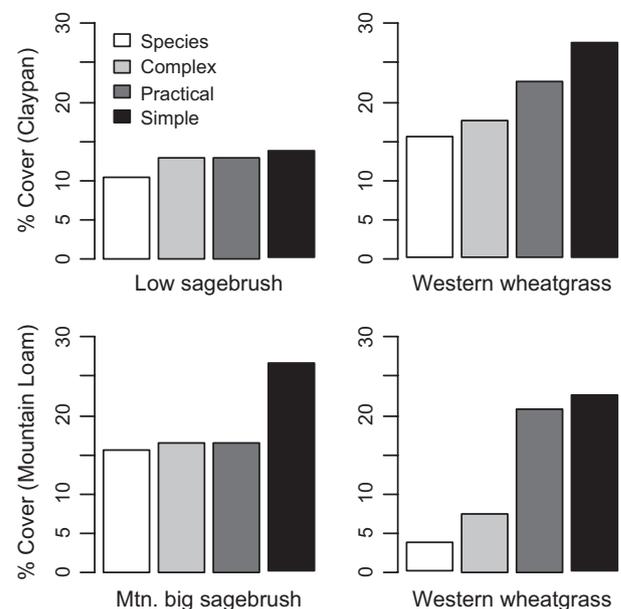


Fig. 2. Average percentage cover of common plant species and their corresponding Complex, Practical and Simple TGs in the Claypan and Mountain Loam ecological sites. Dominant species often make up a majority of their functional group, driving similarities between species- and functional group-defined vegetation patterns and responses to management and environmental variation.

co-dominant species in multiple TGs (Claypan SP5 and SP6) or were characterized by an uncommon shrub (*Artemisia tripartita*; Claypan SP7 and Mountain Loam SP5). Werger & Sprangers (1982) noted that the disagreement between their species- and TG-based classifications of plots tended to be around 'atypical' or 'locally restricted' communities. Unfortunately, diverse plant communities and locally rare species are important for building STMs

because they often characterize 'reference states', or sets of plant communities where ecological processes are operating within their historic range of variation under a natural disturbance regime (Bestelmeyer et al. 2009). These are important for an overall understanding of vegetation dynamics on that ecological site, but are less likely to be distinguished by characteristic trait groups because they are diverse and contain a more balanced composition of different trait groups. An approach to monitoring based on trait group composition may, therefore, miss reference conditions.

Species- and trait-based approaches describe plant community responses to management

We found that species and TG approaches are complementary in describing plant community responses to range management on the two soil types. While they agree in many cases, taking multiple approaches provides a more complete understanding of dynamics than one approach. Differences show that choice of approach will affect interpretation of plant community response to management.

Similar species and TG-defined potential states identified similar relationships to management practices and environmental variables, showing that complex TGs provide some of the same information about sagebrush steppe dynamics as species composition. Responses to management differed on the two soil types. Mountain Loam dense *Artemisia tridentata* subsp. *vaseyana* shrublands (SP1, CO1 and PR1) are all related to higher historic grazing intensity and shallower slopes. Claypan dense *Artemisia arbuscula* subsp. *longiloba* shrublands (SP2, CO2, PR2 and SI2) generally occur on steeper slopes with less clayey soils. Claypan native grasslands (SP1, CO1, PR1 and SI1) are related to chemical shrub treatment (Photo S2). In contrast, spraying Mountain Loam is related to a state with diverse grasses, forbs and shrubs (SP3, CO3; Photo S1). Simple TGs only provided similar information to species composition on one soil type, suggesting that life form-based monitoring will miss important information about sagebrush steppe dynamics.

Trait groups also provided additional information about plant community change that was not revealed by species composition. In some cases, similar potential states did not reveal the same management or environmental driver; for example, Mountain Loam CO4 was related to lower grazing intensity whereas SP4 was related to spraying. In others, TG-defined potential states identified patterns in composition related to management that species-defined potential states did not; for example, Mountain Loam PR2, characterized by Tall Grasses, is related to lower historic grazing intensity. These findings imply that models of vegetation change (such as STMs) that are created using

different approaches will likely describe some different dynamics.

We chose an *a priori* approach to establishing TGs (species are grouped into TGs with similar traits) because direct, concurrent trait measurements in the field were not available for this data set, and because others recommend the use of *a priori* TGs in monitoring (e.g. Pellant et al. 2005). However, we may have missed important intra-specific variation in trait values as a response to management or environmental variation. A comparison of this field approach to species and *a priori* TG approaches would provide important additional information about the usefulness of species vs TG approaches.

Usefulness of the two approaches for describing sagebrush steppe dynamics

Do we lose information about sagebrush steppe dynamics by taking a trait-based rather than a species approach? We do: overall, species composition revealed the most relationships between potential alternate states and range management and environmental variation, especially compared to simple TGs. However, information is also gained by taking a TG approach, because some TG-defined states were related to different management practices and environmental factors than species-defined states (Tables 1 and 2, Appendices S1 and S2). A combination of species and TG approaches gives the most complete understanding of sagebrush steppe dynamics.

Sensitivity of a trait grouping scheme to many different management practices and environmental variables is also useful for describing plant community dynamics. No single classification was related to all management practices or environmental variables on both soil types (Table 3). Sensitivity to management was slightly higher on average for species vs trait groups, while sensitivity to environmental variation was similar for all approaches. Contrasts in sensitivity between the two soil types are related to differences in plant community response to management and environmental variation. For example, sprayed Claypan plots are persistent grassland, whereas sprayed Mountain Loam plots have abundant shrubs and forbs (Kachergis et al. 2012) – thus Claypan response to chemical shrub treatment is expressed in terms of simple TGs (increase in grasses and decrease in shrubs), whereas Mountain Loam response is not. Different dynamics on different soil types reinforce the need to compare areas that are environmentally similar (e.g. soil types or ecological sites; USDA NRCS 2003) when conducting observational studies to describe plant community response to management.

This study reveals that species and trait group composition are both useful for understanding sagebrush steppe response to management. However, there are trade-offs

among approaches, and choice of one vs the other will depend on management and monitoring objectives in addition to practical considerations. Species composition was sensitive to the most different management practices, and should be used when identifying diverse communities or communities characterized by rare species as a priority. However, the time and money required to identify plant species may not be justified when the objective is simply to understand vegetation response to management. TGs that use five or more traits mechanistically related to disturbance identify many of the same vegetation patterns, management effects and environmental influences as species composition. The Complex and Practical TGs used here can be quickly identified in the field with a minimum of training and do not require species identification in order to identify the TG. Simple TGs are only useful in cases where a strong, single life form-based response to disturbance is expected, and may not be substantially faster to identify than more complex TG approaches. Using the most complex TG grouping scheme that is feasible in a particular study will detect a broader range of responses to management and environmental factors than a simpler approach.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Photos S1 and S2. Plots that have undergone chemical sagebrush treatment on the Mountain Loam (A) and Claypan (B) ecological sites, northwestern Colorado, US.

Appendices S1 and S2. Characteristic species and trait groups of potential states of the Mountain Loam and Claypan ecological sites, northwestern Colorado, US. States were defined by species and trait group composition; complexity of trait groups decreases from left to right.