

Can ecological land classification increase the utility of vegetation monitoring data?



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ABSTRACT

Vegetation dynamics in rangelands and other ecosystems are known to be mediated by topoedaphic properties. Vegetation monitoring programs, however, often do not consider the impact of soils and other sources of landscape heterogeneity on the temporal patterns observed. Ecological sites (ES) comprise a land classification system based on soil, topographic, and climate variations that can be readily applied by land managers to classify topoedaphic properties at monitoring locations. We used a long-term (>40 y) vegetation record from southeastern Arizona, USA to test the utility of an ES classification for refining interpretations of monitoring data in an area of relatively subtle soil differences. We focused on two phenomena important to rangeland management in the southeastern Arizona region: expansion of the native tree velvet mesquite (*Prosopis velutina* Woot.) and spread of the introduced perennial grass Lehmann lovegrass (*Eragrostis lehmanniana* Nees). Specifically, we sought to determine if a quantitative, ES-specific analysis of the long-term record would (1) improve detection of changes in plant species having heightened ecological or management importance and (2) further clarify topoedaphic effects on vegetation trajectories. We found that ES class membership was a significant factor explaining spatiotemporal variation in velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density measurements. In addition, we observed that the potential magnitude of velvet mesquite and Lehmann lovegrass increases varied substantially among ES classes. Our study brings attention to a practical land management tool that might be called upon to increase the effectiveness of vegetation-based indicators of ecosystem change.

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1. Introduction

Vegetation monitoring is one of the principal methods used to assess the ecological consequences of management actions and climate change at local to landscape scales (Herrick et al., 2005). Vegetation dynamics at these scales can vary strongly in response to topoedaphic heterogeneity (Bestelmeyer et al., 2011; Pringle et al., 2006; Wu and Archer, 2005). For example, even relatively subtle variations in soil profile properties, such as the depth to clay- or carbonate-rich horizons in otherwise similar soils, can cause variations in rates of shrub encroachment or grass mortal-

ity (Bestelmeyer et al., 2006; Browning et al., 2012). Vegetation monitoring programs, however, often do not consider the impact of topoedaphic heterogeneity on the temporal patterns observed, which can lead to misinterpretation of early warning indicators or the importance of anthropogenic or climatic variables being studied (Pringle et al., 2006).

To address the effects of topoedaphic properties, some authors have recommended that monitoring sites be linked to soil- and climate-based land classification systems (Herrick et al., 2006; Karl and Herrick, 2010) such as the ecological site (ES) classifications used widely in the United States (Brown, 2010; USDA-NRCS, 2013) and similar classifications used worldwide (Blanco et al., 2014; Green and Klinka, 1994; Ray, 2001; van Gool and Moore, 1999). ES classes are subdivisions of a landscape based on soil, topographic, and/or climate properties known to influence veg-

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etation composition and change (Duniway et al., 2010). Each ES class is associated with a state-and-transition model describing the vegetation changes that are likely to occur following specific management actions or natural events (Bestelmeyer et al., 2009; López et al., 2013). Land areas belonging to the same ES class are expected to provide the same general environment for plant establishment and growth. This expectation can give land managers increased confidence that the knowledge they have acquired from a particular vegetation monitoring effort can be effectively applied to other areas belonging to the same ES class (and only cautiously applied to other areas). In addition, the criteria used to differentiate ES classes are in most cases explicitly defined, which enables land managers to assess the degree of similarity between two classes and determine the suitability of applying ecological knowledge across class boundaries. In the United States separate ES classifications are created on a per-region basis, and individual ES classes are typically only utilized in that region they were developed for.

Given the important role of topoedaphic properties in controlling vegetation composition and dynamics, best practices commonly call for the incorporation of topoedaphic strata into vegetation monitoring designs. Use of ES classifications for landscape stratification is likely to increase with official commitment by three prominent US land management agencies – the Natural Resources Conservation Service, Forest Service, and Bureau of Land Management – to utilize ES classifications as a basis for monitoring, assessment, and planning in rangelands (BLM, 2010). ES classifications are already applied to a number of conservation activities and therefore represent a sensible tool for linking monitoring programs to other aspects of land management such as restoration projects and grazing plans. Nevertheless, there has been little empirical study aimed at supporting or refuting the utility of ES classifications with regard to ecosystem monitoring, despite recommendations to further incorporate ES classifications or similar frameworks into vegetation monitoring programs (Bestelmeyer et al., 2009; Herrick et al., 2006; Karl and Herrick, 2010).

We used an uncommonly long (>40 years), well-studied, and spatially extensive monitoring dataset available from the Santa Rita Experimental Range (SRER) to test for differences in vegetation trajectories among ES classes reflecting differences in subsoil properties in sandy soils of piedmont slope landforms. Long-term monitoring of ecological indicators is essential for resolving critical uncertainties in the detection of ecosystem trends, such as whether or not environmental degradation or improvement is taking place in ecosystems, like deserts, that respond slowly or episodically to management or climatic drivers. Increasing the effectiveness of ecological indicators may require addressing topoedaphic variation in a more systematic and detailed way than typically occurred in the past, and ES classification has been identified as one tool that could be used to address topoedaphic variation in such a manner (Bestelmeyer et al., 2009; Herrick et al., 2006). Our study provides a rare, empirical assessment of ES classification utility using an existing long-term monitoring dataset. By associating each SRER monitoring site with an ES class, we sought to determine if the detection of changes in plant species recognized as having heightened ecological or management importance in our study area would be improved. We also sought to determine whether previously unrecognized edaphic effects on vegetation trajectories had the potential to produce erroneous interpretations of vegetation monitoring data and associated indicators of ecosystem change. The ES classes studied here reflect differences in subsoil clay content that would likely go unnoticed by many observers without explicit consideration of ES classes, and earlier published analyses of the SRER long-term monitoring data did not address such soil variations. Finally, our study offered an opportunity to refine interpretations of a high-value long-term dataset and evaluate the need to modify the current ES classification system.

2. Methods

2.1. Focal species

We limited our analysis to two plant species having great management significance in the southeastern Arizona region: velvet mesquite (*Prosopis velutina* Woot.) and Lehmann lovegrass (*Eragrostis lehmanniana* Nees). Velvet mesquite is a small tree native to portions of Arizona, California, and New Mexico. Historically abundant on the SRER primarily along ephemeral drainages, the species has since colonized most upland areas of the research property (McClaran, 2003; McClaran et al., 2010). Expansion of velvet mesquite on the SRER is an example of a more widespread pattern of woody plant encroachment and thickening that has occurred across much of the western United States over the past century (Van Auken, 2000; Van Auken, 2009). Management of woody vegetation continues to be emphasized in many areas, and herbaceous-to-woody type conversions are featured prominently in state-and-transitions models currently described for US rangelands (Twardell et al., 2013).

Native to southern Africa, Lehmann lovegrass was introduced to the SRER and other parts of the southwestern United States to increase livestock forage on degraded rangelands (Cox et al., 1988). Despite its benefits as forage, the species has proven to be an undesirable invader of areas managed to promote native vegetation and associated ecosystem services. The species is known to replace native grasses given suitable climatic and edaphic conditions (Angell and McClaran, 2001; Bock et al., 2007). Like expansion of the native velvet mesquite, the spread of Lehmann lovegrass exemplifies an ecological syndrome affecting large areas of the western United States – the replacement of native plants by invasive nonnative grasses. In some of the more extreme examples of this phenomenon, nonnative grass introduction has resulted in regime shifts from shrub and/or cactus dominated ecosystems to ecosystems dominated by grasses, often with important impacts on plant biodiversity and wildlife habitat (Knapp, 1996; Marlette and Anderson, 1986; Olsson et al., 2012; Whisenant, 1990).

2.2. Monitoring dataset

Permanent vegetation monitoring plots were established on the SRER by several independent and temporally disjointed studies. Monitoring locations were generally not selected in a strictly random or stratified-random fashion. Consistent collection methods enabled data from these plots to be later compiled into a single long-term monitoring dataset, available online from the University of Arizona (<http://cals.arizona.edu/srer/data.html> see On-going Long-Term Measurements; McClaran et al., 2002). Standard measurements performed at each monitoring plot included the total amount of velvet mesquite canopy cover and Lehmann lovegrass basal cover intersecting a single 30.4 m transect. Beginning in 1972, perennial grass density was estimated using plant counts within a 0.3 × 30.4 m belt transect running parallel to, and having one side bounded by, the line-intercept transect. The number of plots revisited on the SRER increased through time as new studies were initiated. Our analysis was limited to velvet mesquite canopy cover measurements collected from 1975 through 2012, Lehmann lovegrass basal cover measurements collected from 1984 through 2012, and Lehmann lovegrass density measurements collected from 1972 through 2012 (at the same 48 plots in each case). These time periods were selected based on our desire to maximize sample sizes while ensuring that the same number of samples were collected at each sample date. We also limited our analysis to those plots not altered by wildfire or intentionally cleared of velvet mesquite during the 41 year analysis period (McClaran and Angell, 2006) to

Table 1

Soil characteristics distinguishing the three ecological site classes most commonly associated with Santa Rita Experimental Range long-term monitoring plots.

Ecological site class	Distinguishing soil characteristics
Loamy upland (LU)	(1) Sandy loam to loam surface textures 2.5–10 cm deep (2.5–20 cm for gravelly sandy loam). (2) Argillic (relatively clay rich) horizons near the surface.
Sandy loam deep (SLD)	(1) Loamy sand to sandy loam surface textures. (2) Sandy loam subsurface texture to at least 100 cm.
Sandy loam upland (SLU)	(1) Sandy loam surface textures at least 10 cm deep (20 cm for gravelly sandy loam). (2) Argillic (relatively clay rich) horizons at shallow depths.

interpret edaphic effects on velvet mesquite and Lehmann lovegrass dynamics more easily.

2.3. Ecological site classes

Each monitoring plot was assigned a single ES class based on characterization of soil pits by an experienced observer (D. Robnett). Soil pits were excavated at a representative point along each monitoring transect, or in the dominant soil type intersected by the transect when more than one soil type was detected. As is the case in many areas, soil maps alone were not sufficient to assign plots to the correct ES class because the mapping resolution is typically 150–200 ha and multiple ES classes can occur within individual map units. Monitoring plots were predominantly associated with loamy upland (LU), sandy loam deep (SLD), and sandy loam upland (SLU) ecological site classes in the 300–400 mm precipitation zone (Land Resource Unit C) of Major Land Resource Area 41. We focused our analyses on these three classes and did not consider plots belonging to the other, less well represented ES classes found on the SRER. As a result, the labels LU, SLD, and SLU refer specifically to ecological sites R041XC313AZ, R041XC318AZ, and R041XC319AZ described in the Ecological Site Information System maintained by the Natural Resources Conservation Service (USDA-NRCS, 2013). In our study area the LU, SLD, and SLU sites occur most commonly on alluvial fans, are intermingled at a landscape level, and represent subtle differences in soil profile development. All three ES classes are typically characterized by loamy sand or sandy loam surface textures (Table 1). Soils of the SLD class, however, are coarse textured to at least 100 cm below the surface, whereas LU and SLU soils exhibit a notable clay increase with depth. The primary difference between LU and SLU ecological sites is the depth of this argillic (relatively clay rich) horizon. State-and-transition models associated with the LU, SLD, and SLU classes indicate the potential for velvet mesquite to invade and increase to as much as 25% canopy cover on all three sites. The same models also describe the potential for the herbaceous understory of all three sites to transition from a native perennial and/or annual grass dominated community to a community dominated by Lehmann lovegrass.

2.4. Statistical analysis

Two complementary approaches were used to test for differences in velvet mesquite and Lehmann lovegrass dynamics among ES classes. Our first approach was to characterize time series data by computing mean and maximum values of velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density recorded at individual plots. The Kruskal-Wallis test was used to identify significant differences in mean and maximum values among and between ES classes.

Our second approach was to distill information from velvet mesquite and Lehmann lovegrass time series using multivariate statistical techniques. Multivariate statistics are commonly employed in plant ecology to assess vegetation differences among study sites based on the presence or abundance (e.g., cover or density) of multiple plant species. We used an analogous approach to compare monitoring plots based on the temporal profile of

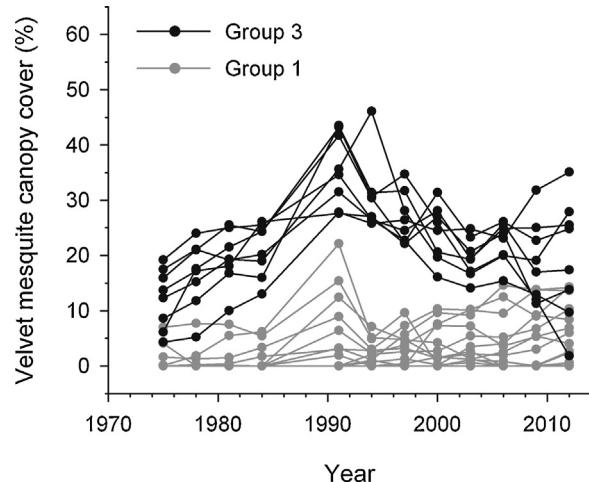


Fig. 1. Example illustrating how monitoring plots were clustered based on their temporal velvet mesquite canopy cover profiles. Each line corresponds to time series data collected at a single monitoring site. Monitoring sites were grouped by considering all measurements in a time series as distinct (potentially correlated) attributes of a particular site. This approach is similar to how multivariate statistics are used in plant ecology to group sample sites based on multiple plant species or in remote sensing to group pixels based on multiple spectral bands. Only two of the four derived clusters are shown here for clarity.

repeated velvet mesquite or Lehmann lovegrass measurements (Potgieter et al., 2007). Multivariate statistics were selected over linear or nonlinear mixed models because of the high degree of variation among sample plots (both within and between ES classes) in initial density/cover values and subsequent trajectories. Separate analyses were performed using repeated measures of velvet mesquite canopy cover, Lehmann lovegrass basal cover, or Lehmann lovegrass density as multiple (potentially correlated) attributes of individual monitoring plots. For all analyses, dissimilarity of plot pairs was computed as the Euclidean distance between plots in multivariate space. Plots exhibiting similar cover or density trends over time were expected to be separated by smaller overall distances. Permutation-based analysis of variance (PERMANOVA; Anderson, 2001) was applied to dissimilarity matrices in order to evaluate the importance of ES class membership as a source of variation (50 000 permutations using the adonis function in the R package vegan; Oksanen et al., 2013). To test if plots within a particular ES class were more dispersed in multivariate space than those belonging to another class, we calculated the distance between each plot and the spatial median of its associated ES class (betadisper function in the R package vegan; Anderson, 2006). Permutation-based analysis of variance was then performed on the resulting distances (10 000 permutations). An alpha level of 0.05 was used for all significance tests, and no effort was made to test for or address non-normal data distributions.

Vegetation trajectories of multiple sample plots can be difficult to visualize and compare using line graphs or other simple graphing techniques. Multivariate cluster analysis enabled us to better visualize differences in velvet mesquite and Lehmann lovegrass dynamics among study plots and ES classes (Fig. 1). Plots were

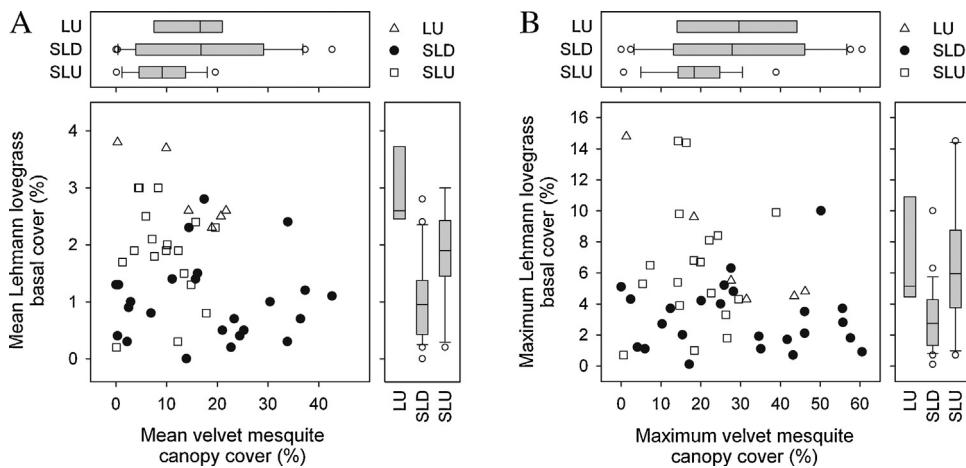


Fig. 2. Comparison of velvet mesquite and Lehmann lovegrass time series summary statistics derived for each SRER monitoring plot. **A**, Mean velvet mesquite canopy cover and mean Lehmann lovegrass basal cover measured over the study period. **B**, Maximum velvet mesquite canopy cover and maximum Lehmann lovegrass basal cover measured over the study period. Analysis periods were 1975–2012 for velvet mesquite canopy cover and 1984–2012 for Lehmann lovegrass basal cover. Box plots indicate the 10th, 25th, 50th, 75th, and 90th percentiles and outliers. LU indicates the loamy upland ecological site class; SLD, sandy loam deep; and SLU, sandy loam upland.

grouped into a predefined number of clusters using the Euclidean dissimilarity matrix described above (*pam* function in the R package *cluster*; Maechler et al., 2013; Reynolds et al., 2006). We then computed 25%, 50%, and 75% quantiles of cover or density measurements for each cluster at each sample date. Numerous statistical methods are available to assess the appropriateness of different cluster solutions, and we explored several of these options to help determine a reasonable number of clusters for our analysis. Plotting three separate measures – within-cluster sum of squares (*kmeans* function in the R package *stats*), mean dissimilarity between cluster members and cluster medoids (*pam* function in the R package *cluster*), and the gap statistic for goodness of clustering (*clusGap* function in the R package *cluster*) – as a function of cluster count generally led to similar interpretations about reasonable cluster numbers (see Appendix A). Prospective cluster numbers were also judged according to their perceived utility for visualizing trends (e.g., a large number of clusters might do little to simplify visualizations).

3. Results

3.1. Time series summary statistics

Compared to SLU plots ($n = 18$), plots assigned to the SLD ($n = 24$) class exhibited a broader distribution of mean and maximum velvet mesquite canopy cover values (Fig. 2). Median values of these two summary statistics were also higher for the SLD class than for the SLU class. Kruskal-Wallis tests indicated a significant difference in mean velvet mesquite canopy cover between SLD and SLU plots and a nearly significant difference ($P = 0.0534$) in maximum canopy cover values between these two ES classes (Table 2). In contrast, LU plots ($n = 6$) could not be distinguished from SLD or SLU plots based on mean and maximum velvet mesquite canopy cover.

Mean and maximum Lehmann lovegrass basal cover and density values were also significantly different between SLD and SLU classes (Table 2). These differences were opposite those observed with velvet mesquite summary statistics, however. In the case of Lehmann lovegrass, median values of both summary statistics were higher for the SLU class than for the SLD class (Fig. 2). Median values tended to be even higher within the LU class. Kruskal-Wallis tests indicated significant differences in all Lehmann lovegrass summary statistics between LU and SLD plots. Mean basal cover and density differed significantly between LU and SLU plots, while maximum basal cover and density did not. Statistical comparisons involving

the LU class, however, may not be highly reliable given the small number of LU plots sampled.

3.2. Multivariate analyses

Results of multivariate analyses were similar to those described above for time series summary statistics. ES class membership was found to be a significant predictor of variation in velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density among monitoring plots through time (see Adonis in Table 3). The amount of variance explained by ES class was, however, rather modest in all cases. Permutation-based analysis of variance indicated partial R^2 values of 0.13, 0.25, and 0.22 for velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density, respectively, when applied to data representing all three ES classes.

We also observed significant differences in the dispersion of plots belonging to different ES classes when either velvet mesquite canopy cover or Lehmann lovegrass basal cover was the focus of our analysis (see BD in Table 3). For velvet mesquite canopy cover, SLD plots were dispersed relatively widely in multivariate space compared to LU and SLU plots. Average distance of SLD plots to the ES class spatial median was 44.1% cover, compared to 28.1% for LU plots and 22.1% for SLU plots. For Lehmann lovegrass basal cover, average distance of plots to the respective ES class spatial median was 4.3% cover for LU plots, 2.9% for SLD plots, and 4.8% for SLU plots. The null hypothesis of homogenous dispersion could not be rejected in the case of Lehmann lovegrass density.

Plots were grouped into four clusters to better visualize variation in velvet mesquite canopy cover trends through time (Fig. 3A). These clusters differed most notably with regard to (1) canopy cover at the start of the time series and (2) the amount of canopy cover change (both increases and decreases) over the study period. Plots with relatively low initial canopy cover tended to exhibit relatively little absolute change in canopy cover (e.g., group 1). The opposite was true for plots with relatively high initial canopy cover (e.g., groups 3 and 4). The four clusters derived using velvet mesquite canopy cover were not evenly represented in the three ES classes studied (Fig. 3B). The two groups characterized by relatively low velvet mesquite cover (groups 1 and 2) were reasonably well represented in all three ES classes. In contrast, the two groups characterized by relatively high cover (groups 3 and 4) did not occur in the SLU class. In addition, the group with the greatest cover (group 4) was only represented in the SLD class.

Table 2

Between-ecological site comparisons of select time series summary statistics (mean and maximum) using the Kruskal-Wallis test.

Ecological site classes	Kruskal-Wallis P-value					
	Velvet mesquite canopy cover (1975–2012)		Lehmann lovegrass basal cover (1984–2012)		Lehmann lovegrass density (1972–2012)	
	Mean	Max	Mean	Max	Mean	Max
All	0.0723	0.1010	<0.0001	0.0019	<0.0001	0.0053
LU, SLD	0.4521	0.8968	0.0006	0.0051	0.0002	0.0082
LU, SLU	0.1171	0.1023	0.0092	0.7138	0.0007	0.2712
SLD, SLU	0.0360	0.0534	0.0018	0.0033	0.0048	0.0127

LU, loamy upland; SLD, sandy loam deep; SLU, sandy loam upland.

Table 3

Between-ecological site comparisons of velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density using PERMANOVA multivariate analyses of variance (adonis function in the R package vegan) and dispersion (BD, betadisper function in the R package vegan). Repeated measures of cover or density were treated as multiple attributes of individual monitoring plots, and pairwise dissimilarity of plots was calculated as the Euclidean distance between plots in multidimensional space.

Ecological site classes	Velvet mesquite canopy cover (1975–2012)			Lehmann lovegrass basal cover (1984–2012)			Lehmann lovegrass density (1972–2012)		
	Adonis R ²	Adonis P-value	BD P-value	Adonis R ²	Adonis P-value	BD P-value	Adonis R ²	Adonis P-value	BD P-value
All	0.132	0.0251	0.0013	0.250	0.0003	0.0349	0.219	<0.0001	0.0843
LU, SLD	0.023	0.4442	0.1090	0.334	0.0002	0.1861	0.288	<0.0001	0.0523
LU, SLU	0.137	0.0363	0.3277	0.082	0.1395	0.7086	0.186	0.0034	0.2257
SLD, SLU	0.130	0.0105	0.0002	0.174	0.0014	0.0094	0.078	0.0266	0.1688

BD, betadisper function; LU, loamy upland; SLD, sandy loam deep; SLU, sandy loam upland.

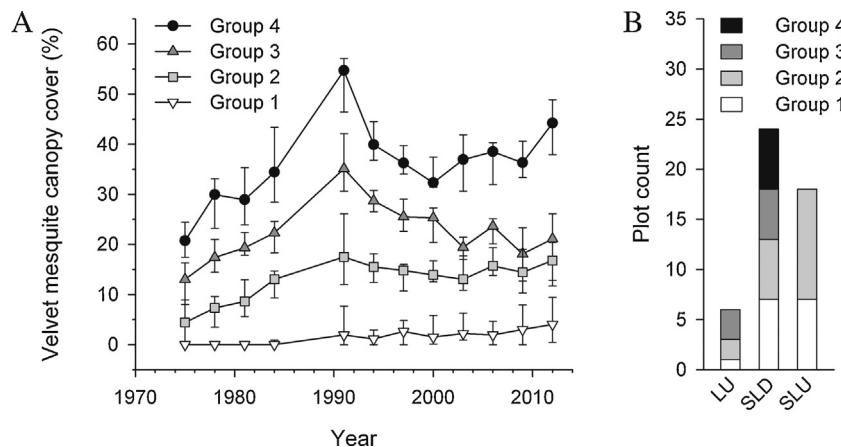


Fig. 3. A, Variation in velvet mesquite canopy cover trends among study plots and ecological site classes. A multivariate clustering routine was used to group plots having similar velvet mesquite canopy cover through time. Symbols indicate median velvet mesquite canopy cover of each group at each sample date, and error bars indicate the 25% and 75% quantiles. B, The number of plots from each group that is represented in each ecological site class. LU indicates the loamy upland ecological site class; SLD, sandy loam deep; and SLU, sandy loam upland.

Four plot clusters (different from those described above) were derived to visualize variation in Lehmann lovegrass basal cover trends (Fig. 4A), and an additional four clusters were derived to visualize variation in Lehmann lovegrass density trends (Fig. 5A). Both vegetation properties tended to follow hump shaped curves that peaked between the years 1990 and 2000. Plot clusters based on these vegetation properties differed most notably with regard to the maximum height of the basal cover or density curve. In the case of Lehmann lovegrass density, another notable difference was the number of plants recorded early in the time series. For basal cover, all four groups (i.e., clusters) were represented in the SLU class, but the group with the greatest Lehmann lovegrass cover (group 4) was not represented in the SLD class, and the group with the lowest cover (group 1) was not present in the LU class (Fig. 4B). In a similar fashion, all four groups derived using Lehmann love-

grass plant density were represented in the SLU class (Fig. 5B). The group exhibiting the least amount of change over time (group 1) was absent from the LU class, but this group made up a larger proportion of the SLD class than did any other group. The group most commonly represented in the SLU class was the group having a relatively high density peak on or around the 1991 sample date (group 3).

4. Discussion

This study utilized a long-term vegetation record from southeastern Arizona to address a simple question: Can a readily-accessed ecological land classification, representing subtle topoedaphic variations that might otherwise go unnoticed by researchers, improve interpretations of vegetation monitoring

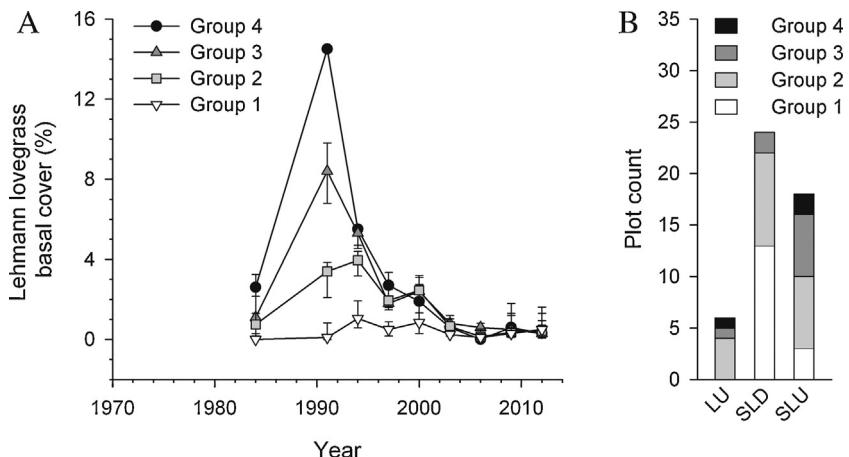


Fig. 4. A, Variation in Lehmann lovegrass basal cover trends among study plots and ecological site classes. A multivariate clustering routine was used to group plots having similar Lehmann lovegrass basal cover through time. Symbols indicate median Lehmann lovegrass basal cover of each group at each sample date, and error bars indicate the 25% and 75% quantiles. B, The number of plots from each group that is represented in each ecological site class. LU indicates the loamy upland ecological site class; SLD, sandy loam deep; and SLU, sandy loam upland.

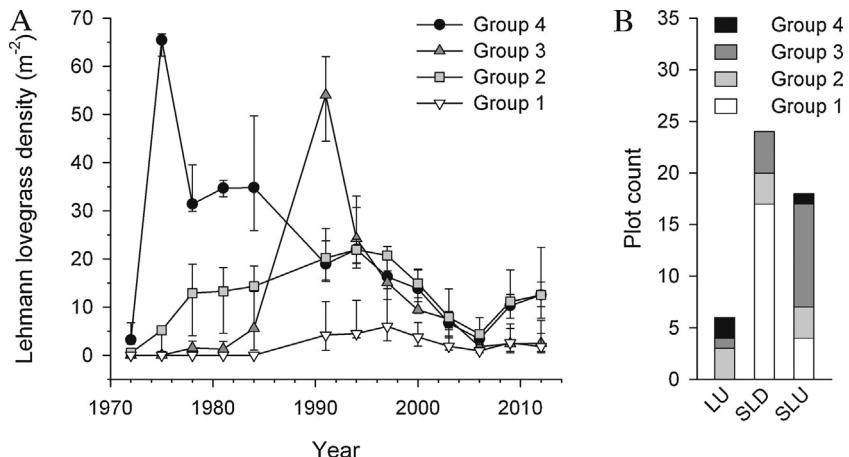


Fig. 5. A, Variation in Lehmann lovegrass density trends among study plots and ecological site classes. A multivariate clustering routine was used to group plots having similar Lehmann lovegrass density through time. Symbols indicate median Lehmann lovegrass density of each group at each sample date, and error bars indicate the 25% and 75% quantiles. B, The number of plots from each group that is represented in each ecological site class. LU indicates the loamy upland ecological site class; SLD, sandy loam deep; and SLU, sandy loam upland.

data? We found that incorporating an ES classification into our analysis of a long-term monitoring dataset helped to explain spatial variations in the magnitude of historical vegetation change, even though overall trends of velvet mesquite and Lehmann lovegrass increase in our study area could be readily interpreted without consideration of ES classes. This result provides a unique example of the potential value of ES classifications and, more broadly, the association of monitoring data with topoclimatic information.

4.1. Overall detection of vegetation change

Early detection of undesirable vegetation change is one potentially important application of vegetation monitoring and associated ecological indicators. Yet, there are instances where a particular change may be less likely to occur or less pronounced in some portions of a landscape compared to others due to geographic variation in topoclimatic properties (Bestelmeyer et al., 2006; Eggemeier and Schwinning, 2009; Molinar et al., 2002; Wu and Archer, 2005). Although monitoring programs that do not account for such topoclimatic variation may be unable to detect important vegetation changes, we found that soil heterogeneity on the SRER was not sufficient to prevent detection of velvet mesquite and Lehmann lovegrass increases during the study period. Our anal-

ysis showed that velvet mesquite increases and Lehmann lovegrass invasion occurred to some extent within all three ES classes studied (Figs. 3, 4, and 5). In addition, the ES classes studied here did not exhibit strongly contrasting patterns of velvet mesquite and Lehmann lovegrass dynamics that could have obscured changes in central tendencies over the study area as a whole. These broad similarities reflect the relatively subtle topoclimatic differences between LU, SLD, and SLU sites and the fact that the sites occur within the same climatic zone.

4.2. Topoclimatic effects on velvet mesquite and Lehmann lovegrass dynamics

Landscape-level characterizations of vegetation change often obscure important spatiotemporal variation at finer scales. Moreover, rates and patterns of vegetation change often have as much management relevance as do shifts in the mere presence or absence of certain plant species. While changes in velvet mesquite and Lehmann lovegrass cover and density were readily observed in the SRER monitoring data irrespective of ES membership, the specific pattern of those changes differed among ES classes (Tables 2 and 3). Two approaches employed here, multivariate analyses and analyses of time series summary statistics, both showed ES class

membership to be a significant factor explaining spatiotemporal variation in velvet mesquite canopy cover, Lehmann lovegrass basal cover, and Lehmann lovegrass density measurements collected over the past ~40 years.

Statistical clustering of monitoring plots based on their temporal trajectories helped to further clarify how vegetation dynamics differed among ES classes. Cluster analyses suggested that measurements associated with a single ES class tended to misrepresent the potential magnitude of velvet mesquite and Lehmann lovegrass increases within the other ES classes. For example, plots having relatively low velvet mesquite canopy cover through time (groups 1 and 2; Fig. 3) occurred in both the SLD and SLU classes, but the two clusters exhibiting the highest velvet mesquite canopy cover (groups 3 and 4) were not represented in the SLU class. Similarly, plots with the smallest increases in Lehmann lovegrass basal cover (groups 1 and 2; Fig. 4) were represented in both the SLD and SLU classes, but plots with the greatest increase of Lehmann lovegrass cover (group 4) did not occur in the SLD class.

These results have four notable, globally-relevant implications for the interpretation of monitoring data and associated ecological indicators. First, because patterns of vegetation change were found to differ among the ES classes studied on the SRER, our results reinforce the potential importance of considering even subtle topoedaphic variation when assessing the magnitude of vegetation change and applying vegetation-based indicators. The development of ecological land class-specific guidelines for interpreting certain ecological indicators could help to reduce misinterpretations arising from topoedaphic effects. Our results also corroborate the value of subdividing the generally sandy soils in the study region into the three ES classes evaluated.

Second, our study illustrates the potential limitations of applying interpretations beyond the specific land types or physical settings being monitored (e.g., Bestelmeyer et al., 2011; Pringle et al., 2006). One of the key premises of ecological land classification-based management frameworks is that future management actions are likely to have more predictable outcomes if information specific to the ecological land classes being managed is available from previous monitoring activities. Our findings support this assertion, indicating that certain information would be lost if observations from a single ES class were used to characterize the dynamics of the other two classes. Additional study is needed to determine if, and how, such information could be used to improve ecosystem restoration strategies or more effectively combat new velvet mesquite or Lehmann lovegrass invasions (e.g., Wonkka et al., 2016).

Third, sufficient sample size is needed in a monitoring effort to represent the central tendency (i.e., mean or median) as well as the variation of vegetation values associated with specific ES classes. Consider, for example, a scenario in which insufficient sample size resulted in the high velvet mesquite cluster (group 4; Fig. 3) being under-represented in the SLD class or the high Lehmann lovegrass cluster (group 4; Fig. 4) being under-represented in the SLU class. In either case, such under-representation would have limited the ability to distinguish the SLU and SLD classes.

Fourth, the length of time represented in the monitoring record will determine the ability to detect differences among ES classes. For example, differences in Lehmann lovegrass cover among ES classes were most apparent prior to 1996, but nearly indistinguishable since. Strong meteorological events are associated with these patterns: the sharp increase of Lehmann lovegrass is associated with very wet conditions in the 1980s, and Lehmann lovegrass decline is associated with prolonged dry and warm conditions since 1996 (McClaran and Wei, 2014). Thus, a longer record improves the ability to identify differences in the potential responses of vegetation among the ES classes.

Our conclusions regarding topoedaphic effects on velvet mesquite and Lehmann lovegrass dynamics are tempered by the recognition that SRER monitoring plots were not established according to a random sampling design, as one would desire if the objective is to extend inference to other parts of the SRER and southeastern Arizona region. Sampling bias alone could conceivably explain the significant difference in velvet mesquite canopy cover reported here between SLD and SLU plots. Our analysis indicated a strong correlation between velvet mesquite measurements taken at different times in the study period, which means that choices made at the outset of a monitoring experiment could have considerable influence on observations later on. Nevertheless, we have little reason to suspect that SRER monitoring locations were selected in a way that favored SLD sites with relatively high velvet mesquite cover, and our findings generally agree with other studies of edaphic effects on velvet mesquite establishment and growth. For example, the spatial distribution of honey mesquite (*Prosopis glandulosa* Torr.) groves and herbaceous openings on the La Copita Research Area in southern Texas was found to align closely with the absence or presence, respectively, of a well-developed argillic soil horizon (Archer, 1995). Similarly, Browning et al. (2008) studied historical mesquite expansion on the SRER using aerial photography and soil mapping data and found that velvet mesquite proliferated more rapidly in sandy map units compared to clayey map units, even though canopy cover on the two soil types eventually converged on similar values over time.

The tendency for velvet mesquite canopy cover to be higher at SLD plots than at SLU plots is also consistent with expectations based on the contrasting hydrological properties of fine and coarse textured soils. Velvet mesquite plants growing on SLD sites are likely to have greater overall access to soil moisture due to the infiltration-promoting characteristics of sandy soils and the relatively extensive root system of this tree species (Fravolini et al., 2005; Noy-Meir, 1973). On the other hand, enhanced surface drying of coarse textured soils may make SLD sites less suitable than SLU sites to relatively shallow rooted herbaceous species such as Lehmann lovegrass. This phenomenon, together with the potential for argillic horizons to reduce moisture loss from the Lehmann lovegrass rhizosphere, may provide a mechanistic explanation as to why SLU plots tended to exhibit greater mean and maximum Lehmann lovegrass basal cover and density over time compared to SLD plots (English et al., 2005). McClaran et al. (2010) suggested a link between deep sandy soils and poor representation of Lehmann lovegrass based on repeated ground photographs taken on the SRER. Edaphic controls on tree:grass ratios have also been identified in African and Australian savannas (Sankaran et al., 2005; Walker and Langridge, 1997). Interestingly, mean and maximum Lehmann lovegrass basal cover and density values recorded at LU monitoring plots tended to be even higher than those recorded at SLU plots, a difference we cannot readily explain using the general models of plant-soil-moisture interactions noted above.

5. Summary

ES classifications have been adopted by land management agencies in the United States and other countries as frameworks for developing land unit-specific management recommendations, models of vegetation dynamics (e.g., state-and-transition models), and protocols for assessing ecosystem health. Monitoring activities, in turn, are recognized as an important tool for collecting information that can be used to support the development, testing, and refinement of vegetation change models, management approaches, and ecosystem health indicators. Monitoring datasets that span relatively long time periods afford unique opportunities to evaluate the utility of existing ES classification schemes. In our analysis of

the SRER long-term vegetation record, we found that two vegetation changes important to land management in the southeastern Arizona region differed significantly between closely-related ES classes common to the study area. While these differences might not be large enough to warrant a reformulation of current land management prescriptions – and overall trends of velvet mesquite and Lehmann lovegrass increase on the SRER could be readily interpreted without consideration of ES classes – they nonetheless illustrate how information about even subtle soil differences can be used to understand spatiotemporal variations in the magnitude of change that were previously unexplained. Post-hoc assignment of monitoring points to ES (or similar) classes and, more effectively, the use of ES classes as strata in the design of new monitoring pro-

grams could help to reduce misinterpretation of monitoring data and contribute to a more comprehensive understanding of landscape dynamics.

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Appendix A.

See Figs. A1 and A2.

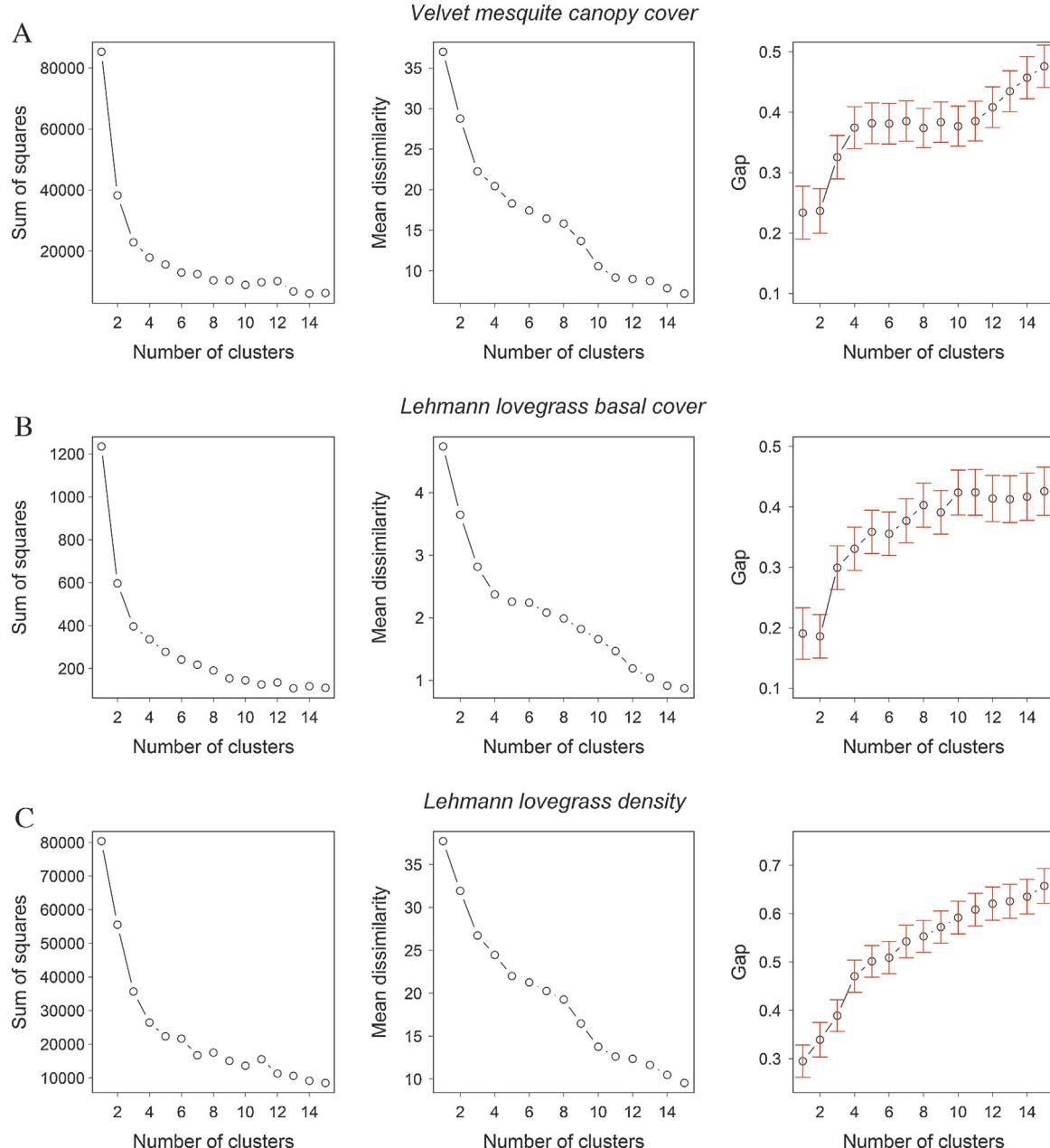


Fig. A1. Three metrics used to help determine a reasonable number of clusters for grouping SRER long-term monitoring plots based on repeated measures of **A** velvet mesquite canopy cover, **B** Lehmann lovegrass basal cover, and **C** Lehmann lovegrass density. Within-cluster sum of squares was computed using the kmeans function in the R package stats. Mean dissimilarity between cluster members and the respective cluster medoid was computed using the pam function in the R package cluster. The gap statistic for goodness of clustering was computed using the clusGap and pam functions in the R package cluster. Each metric was plotted as a function of cluster number, and reasonable cluster numbers were interpreted as those located near the initial bend, or elbow, in the plotted curve. Prospective cluster numbers were also judged according to their perceived utility for visualizing trends. For each vegetation measure studied, we ultimately selected the four-cluster solution to utilize in our analysis.

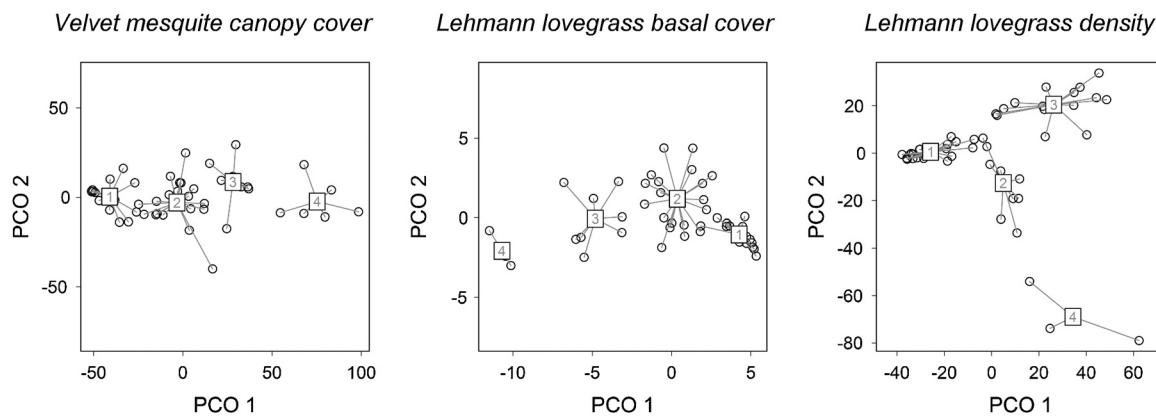


Fig. A2. Example principal coordinates ordination (PCO) diagrams used to help determine a reasonable number of clusters for grouping SRER long-term monitoring plots based on repeated measures of **A** velvet mesquite canopy cover, **B** Lehmann lovegrass basal cover, and **C** Lehmann lovegrass density. For each vegetation measure studied, we ultimately selected a four-cluster solution to utilize in our analysis. Monitoring plots belonging to the same cluster are connected by lines in the PCO diagrams shown here. For velvet mesquite canopy cover, PCO axes 1 and 2 explained approximately 83% and 8%, respectively, of variance in the Euclidean dissimilarity matrix used to cluster monitoring plots. For Lehmann lovegrass canopy cover, PCO axes 1 and 2 explained approximately 74% and 12% of variance. For Lehmann lovegrass density, PCO axes 1 and 2 explained approximately 43% and 31% of variance.

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