



## **Incorporating Diversity Measures into Ecological Site Descriptions to Manage Biodiversity on Heterogeneous Landscapes**

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# Incorporating diversity measures into Ecological Site Descriptions to manage biodiversity on heterogeneous landscapes

By Lina Aoyama, James W. Bartolome, and Lauren M. Hallett

## On the Ground

- We examined whether diversity metrics could be incorporated into the Ecological Site Descriptions and State and Transition Models (ESD-STM) framework to manage multiple goals including biodiversity on heterogeneous landscapes.
- We evaluated plant diversity in two vegetation states (i.e., grassland and shrubland) across three ecological sites in Southern California and found that alpha diversity differed by ecological site and vegetation state.
- Functional diversity remained similar across our three ecological sites.
- Beta diversity between vegetation states was higher than that within each state—in other words, two states support more dissimilar vegetation communities than one state alone.
- Describing both biodiversity metrics and forage values in ESD-STM may help guide conservation planning on working ranches, such as the Tejon Ranch in Southern California.

**Keywords:** Alpha diversity, Beta diversity, ESD-STM, Functional diversity, Shrubs

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## Introduction

Rangelands are spatially and temporally heterogeneous systems, with shrub and grass patches contributing to the landscape level variability. Past range management has focused on controlling or eliminating variability by removing shrubs to increase production of a few dominant key forage species.<sup>1</sup> In the late 20th century, range management has progressed to recognize that multiple stable states exist for many vegetation

types<sup>2</sup> and that the variability in nature is important. Studies have shown that landscape heterogeneity can stabilize biodiversity,<sup>3</sup> plant communities,<sup>4</sup> ecosystem function,<sup>5,6</sup> and even livestock production.<sup>7</sup> However, adoption of landscape heterogeneity as a necessary component of range management has been slow.<sup>8</sup> Theoretically, landowners who embrace landscape heterogeneity could manage for multiple optima (i.e., biological conservation and livestock production) rather than a single optimum. To do that, a conceptual model that communicates how heterogeneity of a landscape could be leveraged to meet multiple management goals is needed.

Working on heterogeneous landscapes, rangeland scientists have developed several land classification systems to conceptually group land areas into units.<sup>9</sup> Early concepts such as range condition<sup>10</sup> were models based on the successional theory of Clements,<sup>11</sup> which was developed for the North American prairie and applied to range management by Sampson.<sup>12</sup> Those models assumed that a given range site potentially has a single stable and recognizable climax vegetation with a corresponding excellent range condition under good grazing management. Experience with other arid rangelands led to the conclusion that the previous models did a poor job of predicting the consequences of management decisions.<sup>13</sup> Westoby et al.<sup>13</sup> proposed State and Transition Model (STMs) that better described the nonequilibrium dynamics observed on semiarid and arid rangelands. Their approach was incorporated into the modification of range sites and range condition to Ecological Site Descriptions (ESDs) by the National Resources Conservation Service (NRCS).<sup>9</sup> ESDs characterize distinctive land units by similar soil, topography, vegetation, and responses to management.<sup>13</sup> Within ESDs, plant community dynamics are represented by simple, box-and-arrow diagrams called STMs, which consist of “states” (stable, long-term ecological conditions), “phases” (plant assemblages within states), and “transitions” (the drivers and mechanisms of changes between states).<sup>13</sup> These models not only communicate the ecosystem dynamics of a given place but enable range managers to test their hypotheses about

alternative states in response to management or the lack thereof.

Despite the growing interest to manage rangelands for biological conservation, current ESDs insufficiently describe the biodiversity—this study focuses on plant diversity—within and across states. An ESD usually includes information about plant species composition (the identity of species present in a community),<sup>9</sup> but there are other ways to measure biodiversity: alpha diversity (species richness and evenness), functional diversity (e.g., exotic grass, native forbs), and beta diversity (turnover in community structure). For example, an ecological site with grass-dominated and shrub-dominated communities has a higher beta diversity than that with only a grass-dominated community. These metrics are often just local, yet range managers are dealing with resource management at the landscape level. Incorporating diversity metrics in ESDs allows the range managers to evaluate biodiversity across the landscape. We believe the ESD framework is conducive to biological conservation because biodiversity is influenced by landscape features like topography and habitat types. For example, McCain and Grytnes<sup>14</sup> found that many plant studies in their overview of elevational richness patterns displayed mid-elevational peaks along increasing elevational gradients. Furthermore, Casado et al.<sup>15</sup> showed greater species richness in grassland than shrubland in Mediterranean rangelands, as species richness in grassland is dependent on space occupied by herbaceous plants, whereas species richness in shrubland is controlled by multiple factors such as shade from woody cover and litter. Organizing biodiversity metrics by landscape features of ecological sites could guide prioritization of areas for biological conservation.

Management of a shrub-grass mosaic is contentious among range managers due to the trade-off between forage production and conservation of shrubs. Because shrubs are less desirable livestock forage than grasses or forbs, aggressive management in attempt to reverse shrub expansion has been applied in North America and Australia since the 1940s, though its cost-effectiveness has been questioned.<sup>16</sup> On the other hand, some landowners recognize that shrubs are worth conserving for their ecological role or for the ecosystem services they provide (e.g., habitat, shelter, and food for wildlife; nectar for pollinators; and carbon storage above and belowground).<sup>17</sup> The ESD-STM framework is not only useful for understanding the drivers of vegetation shifts from one community to another,<sup>18</sup> but also for meeting livestock production and conservation goals on a heterogeneous landscape.<sup>19</sup>

The importance of shrubs in grass-dominated states and shrub-dominated states are inadequately described in most of the ESD-STMs in southern California even though 912 shrub species are native to California. Shrub-grassland conversions are known to occur in both directions in Californian rangelands,<sup>20,21</sup> yet the stability of either state is not known. Describing the states is an important step to maintaining landscape heterogeneity. We added shrub states and assessed

biodiversity for each state in the ESDs described by Spiegel et al.<sup>19</sup> for Tejon Ranch in Kern County, CA – where promoting biodiversity is one of their management priorities. We hypothesized that alpha diversity would vary by ecological sites but functional diversity would remain consistent across the landscape. Specifically, we expected higher alpha diversity in grassland states than shrubland states, but similar functional diversity in grassland states and understory of shrubland states. We also hypothesized higher beta diversity between states than within states—in other words, landscapes with both states would have higher beta diversity than those with one state alone.

## Methods

### Study site

Our study site (8,094 ha [20,000 acres]) was the northwestern portion of Tejon Ranch in Kern County, California, where the San Joaquin Valley meets the Tehachapi Mountains (Fig. 1). Tejon Ranch lies at the intersection of two major land resource areas (MLRA) defined by the USDA: MLRA 17 Sacramento and San Joaquin Valleys and MLRA 18 Sierra Nevada Foothills. Elevation ranged from 45 to 400 m (147 to 1312 feet) above sea level. Slopes were from 0° to 50° with varying aspects (north, northwest, and southwest aspects). Climate is representative of the Mediterranean region, with cool and wet winters and warm and dry summers. Annual precipitation averaged across the study area ranged from 178 to 305 mm (7 to 12 inches) during 1981–2010; annual precipitation in 2017 was 305 mm (12 inches).<sup>22</sup> The main vegetation type was San Joaquin Valley grassland and shrubland.<sup>23</sup> Before the invasion of non-native annual grasses such as ripgut brome (*Bromus diandrus*) and wild oat (*Avena barbata*), the base of the Tehachapi Mountains was dominated by lupines (*Lupinus nanus*) and saltbush (*Atriplex polycarpa*), and the slopes by native perennial bunchgrasses and blue oak savanna.<sup>23</sup> Cattle and sheep were introduced to the study area in the 1840s. For the duration of the study, cattle grazed the study area year-round.

### Study design and measurements

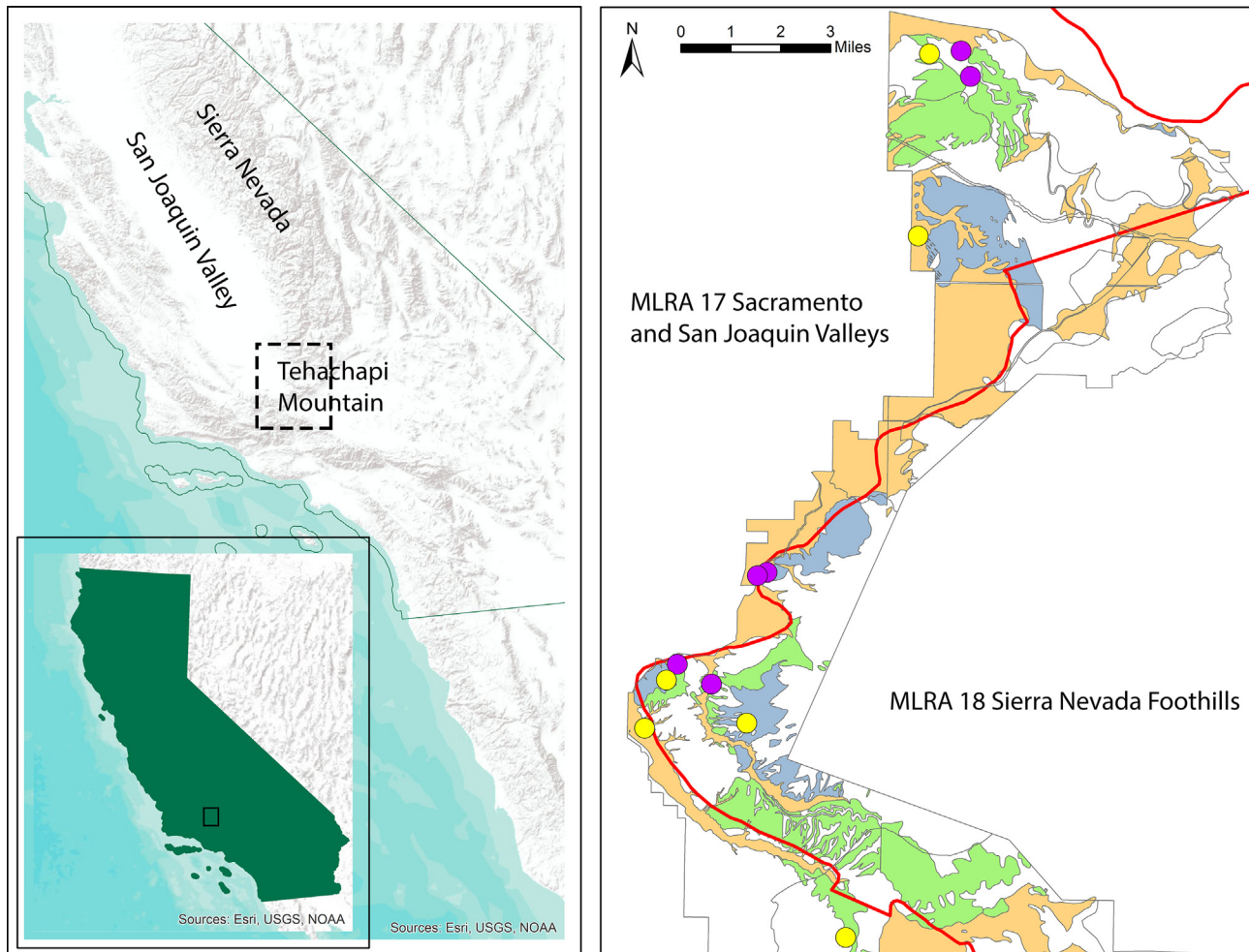
We selected six grassland plots that Spiegel et al.<sup>16</sup> established to describe three ecological sites at Tejon Ranch. We established 6 additional plots in those ecological sites distinguished by geologic substrate, slope group, and elevation group. Each plot comprised a 100-m<sup>2</sup> relevé (20 m × 5 m [65.6 ft × 16.4 ft]) that covered a uniform landform, so the linkages between plant species and the environmental factors measured at the plot level could scale up to the ecological site level. Four 25-m (82-foot) transects radiated in cardinal directions from each corner of the relevé. We measured plant composition using the line-point intercept method<sup>24</sup> recording species or objects (e.g., pebble, bare ground, cattle feces) every 0.5 m (1.6 feet) along these

transects (200 points per plot) in March 2017 and 2018. The line-point intercept method tends to miss rare species but estimates of rare species were not of interest.<sup>24</sup>

In June 2017, we clipped peak herbaceous biomass from three 1-m<sup>2</sup> (10-foot<sup>2</sup>) quadrats at each relevé and oven-dried them at 65 C (149 °F) for 10 days before weighing. From each quadrat, we sampled soil from the top 0 to 15 cm (0 to 5.9 inches) using a 5.7 cm (2.2 inches) diameter corer ( $n = 36$ ). We removed any gravel from the soil samples, air-dried them for 24 hours, and passed the samples through a 2-mm sieve to remove coarse rocks and roots. Bulk density was calculated by dividing the oven-weight (105 C [221 °F] for 12 hours) of 5 ml (0.17 fluid ounces) of soil sample by its volume. Soil pH was measured using a handheld pH meter in a mixed solution of 15 g (0.5 ounces) of sieved soil and 30 ml (1.0 ounces) of deionized water. Soil texture was determined by the hydrometer method.<sup>25</sup> We sent subsamples of sieved soil to the UC Davis Analytical Lab for the following measurements: Na<sup>+</sup>, Ca<sup>2+</sup>, K<sup>+</sup>, Mg<sup>2+</sup>, PO<sub>4</sub><sup>3-</sup>, and SO<sub>4</sub><sup>2-</sup>.

## Statistical analysis

We confirmed the ecological site groupings by principal component analysis (PCA) of physiographic variables (i.e., geology, slope, and elevation) and soil variables. Soil data was normalized by subtracting the mean from each variable and dividing it by the standard deviation. Non-species objects like litter, cow feces, and small mammal bioturbation were removed from the plant community data. To test for differences in plant species composition between each pair of ecological sites, we used the multiple response permutation procedure (MRPP) with the Bray-Curtis distance measure.<sup>26</sup> Plant community phases in the STM were defined by running hierarchical, agglomerative clustering on plant composition data. Data were square-root transformed to give more weight to species with low frequency, and we computed a Bray-Curtis distance measure for each ecological site.<sup>26</sup> Clusters were made using the average-linkage algorithm with 0.6 as the standard cut-off height, which retained clusters known to be ecologically significant.<sup>16</sup>



**Figure 1.** Tejon Ranch study area, Kern County, California, USA. Grassland plots (yellow dots) and shrubland plots (purple dots) were stratified by three ecological sites: San Joaquin Valley Holocene Flats (orange), Lower Miocene Hills (green), and Upper Miocene Hills (blue). MLRA 17 Sacramento and San Joaquin Valleys is shown on the left of the red line, and MLRA 18 Sierra Nevada Foothills is shown on the right.

To compare diversity among ecological sites, we quantified alpha and functional diversity in each plot and beta diversity in each pair of plots in ecological sites. Alpha diversity was measured by species richness (i.e., count of species), native plant species richness (i.e., count of native species),<sup>27</sup> and species evenness using the Shannon Diversity Index.<sup>28</sup> Functional diversity (i.e., perennial and annual forbs and grasses) was measured with and without shrubs to compare functional diversity in grassland and understory shrubland.<sup>29</sup> We focused on functional groups of native species because native species have more conservation value than non-native species. Beta diversity or turnover of community structure was measured by the Bray-Curtis Dissimilarity Index between and within grassland and shrubland states in each ecological site.<sup>30</sup> The effects of ecological sites and states (i.e., grassland and shrubland) on all diversity metrics were quantified using two-way ANOVA (year included as a random effect) followed by a post hoc Tukey test (means considered significant at  $P \leq 0.05$ ). To measure the change of diversity metrics along an elevational gradient, linear regression models were fitted to the data. When comparing species richness in grassland and shrubland, we also used rarefaction curves to account for differences in size among individual plants (herbaceous plants were smaller than shrub plants) and sample sizes (grasslands had less bare ground than shrublands). All statistical analyses were done in R version 3.5.1.<sup>31</sup>

## Results

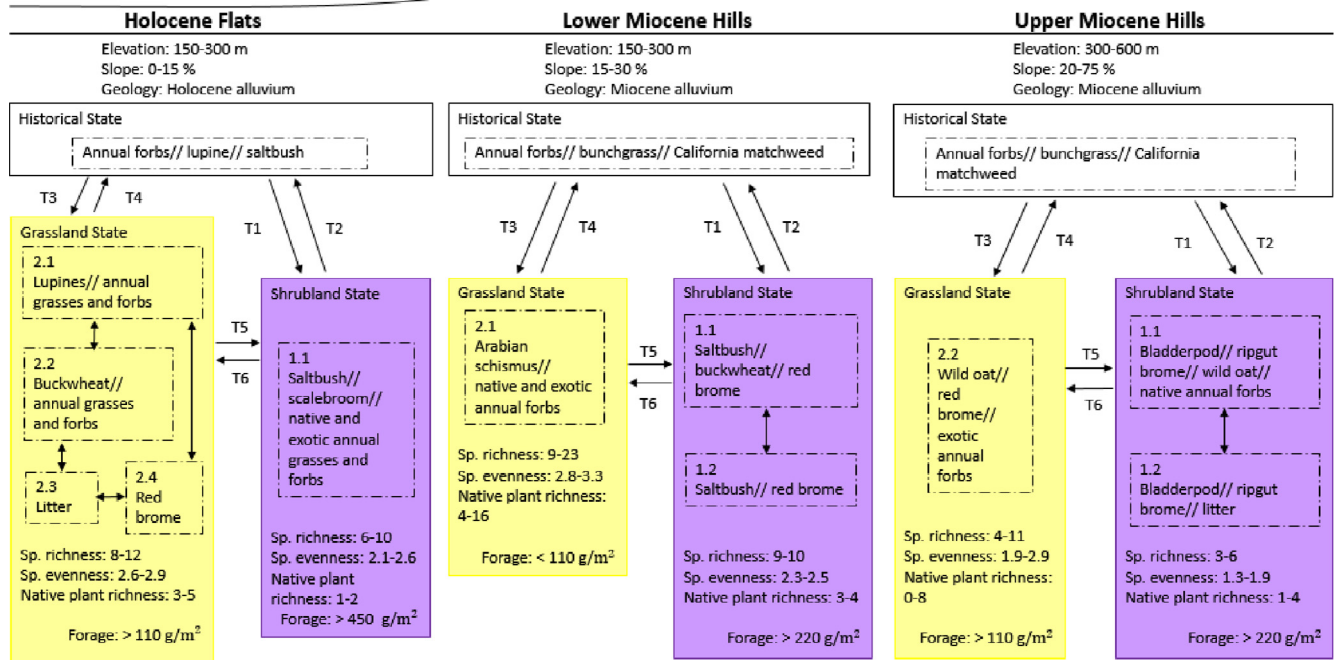
### Ecological site descriptions and state transition models

Multiple states (grassland and shrubland) were present (Fig. 2) in three ecological sites proposed by Spiegel et al.<sup>19</sup>: Holocene Flats, Lower Miocene Hills, and Upper Miocene Hills (Fig. 3). We confirmed that ecological sites differentiated by soil texture and nutrients, specifically sand, silt, and calcium using PCA (Fig. 4). The MRPP analysis verified that plant composition significantly varied between each pair of ecological sites. Observed delta (0.583) was smaller than expected delta (0.655) and chance-correlated within-group agreement was  $>0$  (0.109), which means plant composition was more similar within ecological sites than across all plots.

Holocene Flats Ecological Site was on a Holocene alluvium plain at the base of the Tehachapi Mountains. Its shrubland state contained a saltbush (*Atriplex polycarpa*) and scalebroom (*Lepidospartum squamatum*) mixed community, in which the understory was dominated by non-native grasses including ripgut brome and red brome (*B. madritensis* spp. *rubens*; Fig. 3). Its annual grassland state was composed of four phases including a lupine community, a California buckwheat (*Eriogonum fasciculatum* var. *polifolium*) community, litter-dominated grassland, and red brome-dominated grassland (Fig. 3).



**Figure 2.** Example photos of **A**, San Joaquin Valley Holocene Flats grassland; **B**, Lower Miocene Hills grassland; **C**, San Joaquin Valley Holocene Flats shrubland; and **D**, Lower Miocene Hills shrubland from March 2017 on Tejon Ranch, Kern County, California.



**Figure 3.** Schematic diagram of ecological site descriptions and state-and-transition models on Tejon Ranch, Kern County, California. Solid lined boxes represent states and dashed lined boxes represent phases. Content of states and phases were determined by a clustering analysis of plant composition data. The arrows represent shifts between states or phases. Numbers at bottom right corner of current shrubland state and grassland state boxes represent the average peak herbaceous biomass in June 2017. Transitions from historical state to shrubland state (T1) were likely from lack of fire, and those to annual grassland state (T3) occurred from the invasion of exotic species beginning in the 18th century.<sup>40</sup> The reversal to historical state (T2 and T4) is unlikely even with intentional restoration.<sup>19</sup> Shifts of shrubland states from grassland states (T5) may be possible with planting.<sup>15</sup> Much of the shrubland states transitioned to annual grassland states (T6) in the 19th and 20th centuries, facilitated by cultivation, livestock grazing, and increased fire frequency and intensity associated with elevated fuel loading from exotic annuals.<sup>41</sup>

Lower Miocene Hills Ecological Site was on a Miocene alluvium at the footslope of Tehachapi Mountains. There were two phases in its shrubland state: a saltbush and buckwheat (*E. fasciculatum* var. *polifolium*) mixed community and a saltbush community. Non-native annual grasses and native forbs dominated its grassland state (Fig. 3). Lower Miocene Hills had the highest number of species among ecological sites (Table 1).

Upper Miocene Hills Ecological Site was on a Miocene alluvium at the backslope of Tehachapi Mountains. The shrubland state consisted of two phases of the bladderpod (*Peritoma arborea* var. *globosa*) community (Fig. 3). The grassland state was dominated with non-native annual grasses found in the understory of shrubland state: ripgut brome and wild oat (*Avena barbata* and *A. fatua*; Fig. 3).

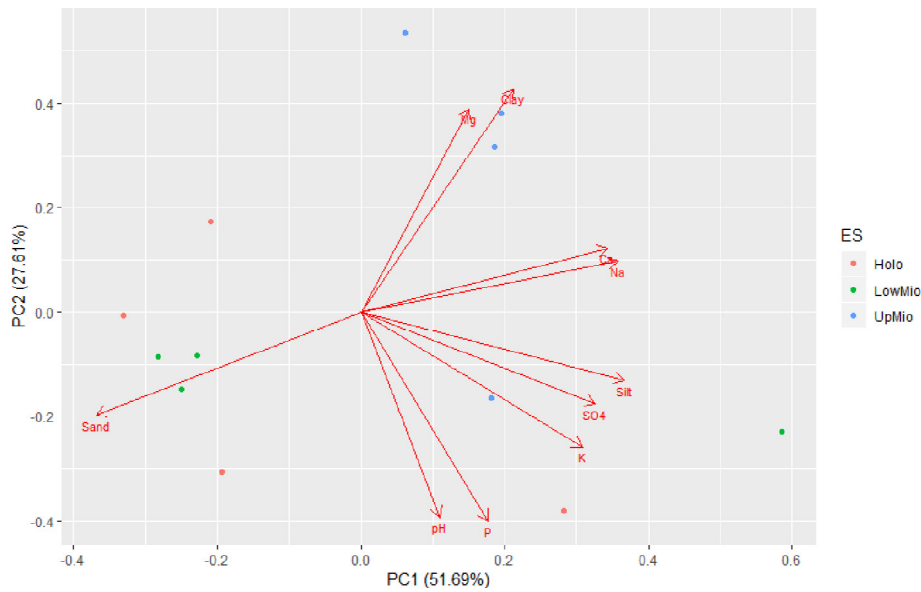
### Alpha diversity

Alpha diversity at the plot level varied across ecological sites and states (Table 2). Species richness, native plant richness, and species evenness (Shannon's Diversity Index) were highest

in the Lower Miocene Hills Ecological Site (Fig. 5). Grassland states were consistently more species diverse than shrubland states (Fig. 5), though this conclusion was not definitive because the sample-based rarefaction curves differentiated by ecological states only in Upper Miocene Hills Ecological Site (Fig. 6). Elevation did not have a significant effect on species richness ( $P = 0.31$ ), native species richness ( $P = 0.77$ ), or Shannon's Diversity Index ( $P = 0.81$ ).

### Functional diversity

States had a significant effect on native annual forbs and native perennial shrubs (Table 2). Native annual forbs were significantly more abundant in grassland states than shrubland states, and native perennial shrubs were significantly more abundant in shrubland states than grassland states (Fig. 7). A native annual grass, small fescue (*Festuca microstachys*), was only found in the Lower Miocene Hills Ecological Site. When shrubs were removed from the analysis, grassland states and the understory of shrubland states had similar functional diversity across ecological sites. None of the native functional



**Figure 4.** Principal component analysis (PCA) plot of soil properties by ecological sites at Tejon Ranch, Kern County, California. Red arrows are pointing at the direction of PCA loadings. The first and second axes explain 51.69% and 27.61% of the variation in soil properties, respectively. ES indicates ecological site; Holo, San Joaquin Valley Holocene Flats ecological site; LowMio, Lower Miocene Hills ecological site; UpMio, Upper Miocene Hills ecological site.

**Table 1. List of grass, forb, and shrub species by ecological site and state detected in March 2017 and March 2018 at Tejon Ranch, Kern County, California. ES indicates ecological site.**

	Holocene Flats ES	Lower Miocene Hills ES	Upper Miocene Hills ES
Grassland state	<i>Acmispon wrangelianus</i>	<i>Acmispon wrangelianus</i>	<i>Amsinckia eastwoodiae</i>
	<i>Amsinckia eastwoodiae</i>	<i>Ambrosia salsola</i>	<i>Amsinckia intermedia</i>
	<i>Avena barbata</i>	<i>Amsinckia menziesii</i>	<i>Amsinckia tessellata</i>
	<i>Bromus madritensis</i>	<i>Astragalus lentiginosus</i>	<i>Avena barbata</i>
	<i>Bromus rubens</i>	<i>Avena barbata</i>	<i>Avena fatua</i>
	<i>Crassula connata</i>	<i>Brassica tournefortii</i>	<i>Bromus diandrus</i>
	<i>Erodium brachycarpum</i>	<i>Bromus diandrus</i>	<i>Bromus madritensis</i>
	<i>Erodium cicutarium</i>	<i>Bromus madritensis</i>	<i>Claytonia perfoliata</i>
	<i>Erodium moschatum</i>	<i>Bromus rubens</i>	<i>Dichelostemma capitatum</i>
	<i>Festuca myuros</i>	<i>Castilleja exserta</i>	<i>Erodium cicutarium</i>
	<i>Gilia tricolor</i>	<i>Crassula connata</i>	<i>Erodium moschatum</i>
	<i>Holocarpha sp.</i>	<i>Deinandra pallida</i>	<i>Festuca myuros</i>
	<i>Hypochaeris glabra</i>	<i>Dichelostemma capitatum</i>	<i>Hordeum murinum</i>
	<i>Plagiobothrys canescens</i>	<i>Eriastrum pluriflorum</i>	<i>Lactuca serriola</i>
	<i>Plagiobothrys nothofulvus</i>	<i>Eriogonum angulosum</i>	<i>Peritoma arborea</i>
	<i>Schismus arabicus</i>	<i>Erodium cicutarium</i>	<i>Phacelia tanacetifolia</i>

Table 1 (continued)

	Holocene Flats ES	Lower Miocene Hills ES	Upper Miocene Hills ES
	<i>Trifolium albopurpureum</i>	<i>Erodium moschatum</i>	<i>Plagiobothrys canescens</i>
		<i>Festuca microstachys</i>	<i>Trifolium willdenovii</i>
		<i>Festuca myuros</i>	
		<i>Gilia tricolor</i>	
		<i>Hemizonia sp.</i>	
		<i>Hollisteria lanata</i>	
		<i>Hordeum murinum</i>	
		<i>Isocoma acradenia</i>	
		<i>Lepidium nitidum</i>	
		<i>Logfia filaginoides</i>	
		<i>Lupinus nanus</i>	
		<i>Mirabilis laevis</i>	
		<i>Pectocarya penicillata</i>	
		<i>Phacelia sp.</i>	
		<i>Plagiobothrys arizonicus</i>	
		<i>Plagiobothrys canescens</i>	
		<i>Plagiobothrys sp.</i>	
		<i>Schismus arabicus</i>	
Shrubland state	<i>Atriplex polycarpa</i>	<i>Amsinckia menziesii</i>	<i>Amsinckia intermedia</i>
	<i>Bromus diandrus</i>	<i>Atriplex polycarpa</i>	<i>Avena barbata</i>
	<i>Bromus hordeaceus</i>	<i>Avena barbata</i>	<i>Avena fatua</i>
	<i>Bromus madritensis</i>	<i>Bromus diandrus</i>	<i>Bloomeria crocea</i>
	<i>Bromus rubens</i>	<i>Bromus hordeaceus</i>	<i>Bromus diandrus</i>
	<i>Centaurea melitensis</i>	<i>Bromus madritensis</i>	<i>Claytonia sp.</i>
	<i>Crassula connata</i>	<i>Bromus rubens</i>	<i>Dichelostemma capitatum</i>
	<i>Erodium cicutarium</i>	<i>Centaurea melitensis</i>	<i>Hordeum murinum</i>
	<i>Erodium moschatum</i>	<i>Crassula connata</i>	<i>Peritoma arborea</i>
	<i>Eschscholzia californica</i>	<i>Eriogonum fasciculatum</i>	
	<i>Festuca myuros</i>	<i>Erodium brachycarpum</i>	
	<i>Hordeum murinum</i>	<i>Erodium cicutarium</i>	
	<i>Isocoma acradenia</i>	<i>Eschscholzia californica</i>	
	<i>Plantago sp.</i>	<i>Festuca microstachys</i>	
	<i>Schismus arabicus</i>	<i>Festuca myuros</i>	
		<i>Hordeum murinum</i>	
		<i>Isocoma acradenia</i>	

(continued on next page)



Table 1 (continued)

	Holocene Flats ES	Lower Miocene Hills ES	Upper Miocene Hills ES
		<i>Lupinus bicolor</i>	
		<i>Melilotus indicus</i>	
		<i>Phacelia sp.</i>	
		<i>Philago sp.</i>	
		<i>Trifolium sp.</i>	

**Table 2. Results of two-way ANOVAs on alpha (i.e., mean species richness, mean native species richness, and mean species evenness), functional (i.e., mean proportion of native annual forbs, native annual grasses, native perennial forbs, and native perennial shrubs), and beta diversity metrics between ecological sites (ES), states (State) and their interactions (ES:State). Sample size = 48 (12 plots × 4 transects per plot). Statistical significance: \* < 0.05, \*\* < 0.01, \*\*\* < 0.001. See text for details on how each metric was calculated.**

Response	Explanatory	F	P-value
Species richness	ES	6.55	0.007**
	State	8.10	0.01*
	ES:State	1.04	0.37
Native species richness	ES	4.12	0.03*
	State	6.52	0.02*
	ES:State	1.36	0.28
Species evenness	ES	12.43	<0.001***
	State	41.13	<0.001***
	ES:State	1.44	0.26
Native annual forbs	ES	0.14	0.87
	State	14.25	0.009
	ES:State	0.18	0.83
Native annual grasses	ES	1.99	0.21
	State	0.006	0.94
	ES:State	0.006	0.99

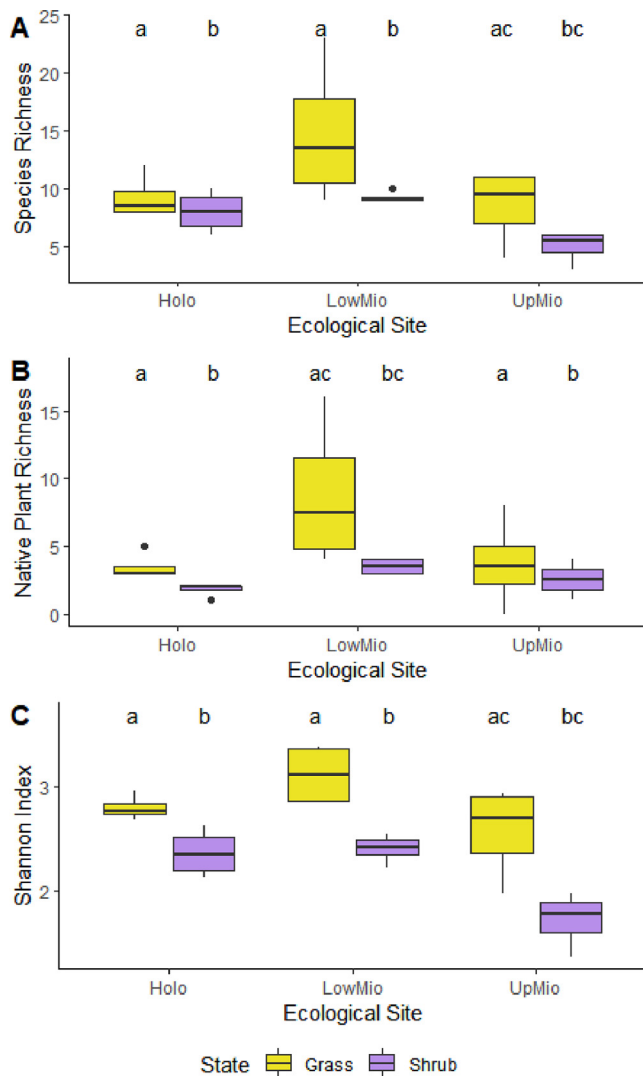
Table 2 (continued)

Response	Explanatory	F	P-value
Native perennial forbs	ES	0.59	0.58
	State	1.23	0.31
	ES:State	0.40	0.68
Native perennial shrubs	ES	1.15	0.37
	State	7.89	0.03*
	ES:State	1.59	0.27
Beta diversity	ES	2.03	0.16

groups were correlated with elevation: annual grass ( $P = 0.29$ ), annual forbs ( $P = 0.56$ ), perennial forbs ( $P = 0.15$ ), or perennial shrubs ( $P = 0.16$ ).

### Beta diversity

Turnover in community structure (beta diversity) measured by the Bray-Curtis Dissimilarity Index was not significantly different among ecological sites (Table 2). Beta diversity between grassland and shrubland states was higher than within states, which means two states support more community structure dissimilarity than one state alone (Fig. 8). Beta diversity decreased with elevation but was not significant ( $P = 0.07$ ).



**Figure 5.** Alpha diversity varied by ecological sites and states (grassland and shrubland). Species diversity was measured as **A**, species richness (i.e., number of species); **B**, native species richness; and **C**, species evenness using the Shannon Diversity Index. Higher values of the Shannon Diversity Index indicate a more even distribution of species in the community. Any two means sharing a letter are not statistically different using the Tukey test. The boxplot indicates the median (center line), the first and third quartiles (box), and distant quartiles (whiskers). The sample size was 48 (12 plots  $\times$  4 transects per plot). Holo indicates San Joaquin Valley Holocene Flats ecological site; LowMio, Lower Miocene Hills ecological site; UpMio, Upper Miocene Hills ecological site.

## Discussion

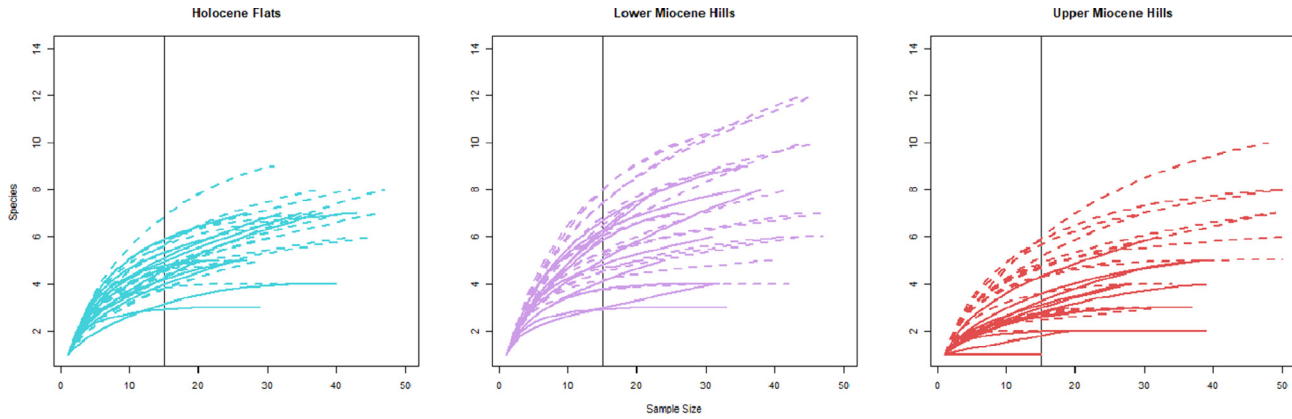
Californian Mediterranean grasslands are considered biodiversity hotspots, and livestock grazing is being increasingly used to promote native species diversity at both the pasture and landscape scales.<sup>32</sup> The ESD-STM framework offers a convenient way to manage multiple resources on heteroge-

neous landscapes, especially important for managers of large properties.<sup>33</sup> Our study at Tejon Ranch is the first case study to organize plant composition and diversity indices in ESDs. We described shrub states in existing ESDs on the western slopes of the Tehachapi Mountains, and found that alpha diversity varied significantly by ecological site and states (grassland and shrubland) but functional diversity remained similar across the landscape. From higher beta diversity between states than within states, we can infer that both grassland and shrubland states contribute to the overall biodiversity of the landscape. In a similar study that compared species diversity by ecological sites, Hendrickson et al.<sup>34</sup> investigated the impact of prairie dogs on the plant communities and forage production. They found that the ecological site framework is a useful communication tool to display trade-offs of species richness, evenness, and forage production simultaneously.

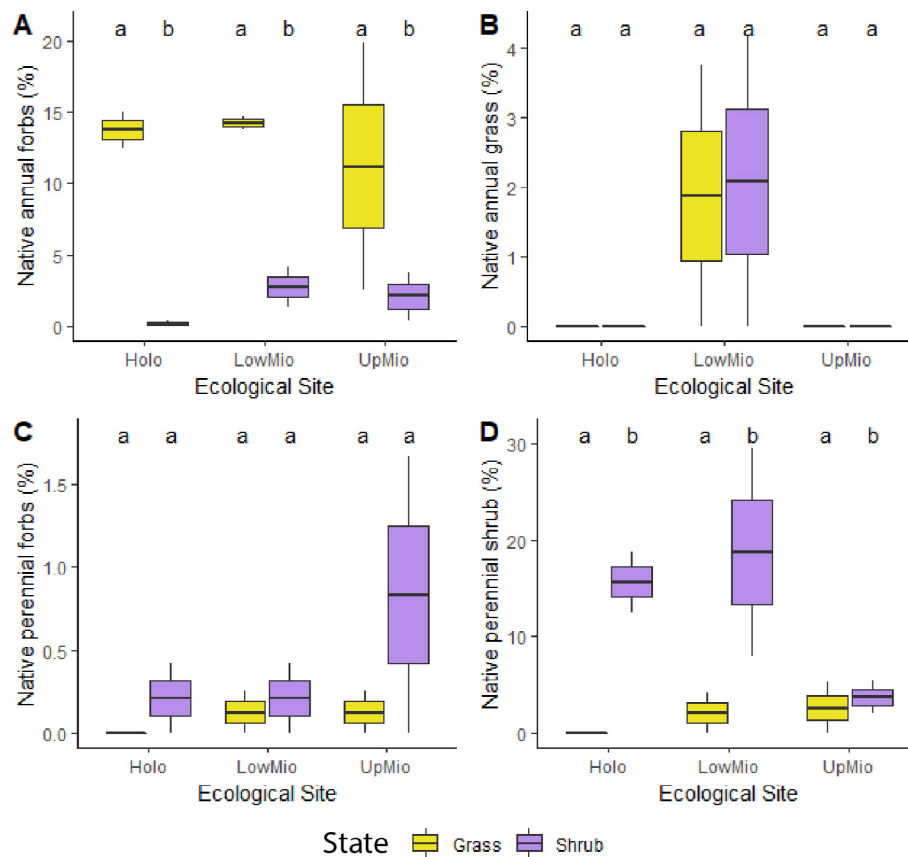
Alpha diversity varied by ecological sites, with the mid-elevation ecological site having the greatest alpha diversity. We believe that the elevations with the warmest-wettest conditions should harbor the highest species richness; thus on arid mountains (e.g., southwestern US mountains), water availability follows a unimodal relationship with elevation.<sup>14</sup> We were not able to relate species diversity with climatic conditions, as in McCain and Grytnes<sup>14</sup> which analyzed the patterns in species richness with elevation that ranged from 0 to 3,000 m (0 to 10,000 feet), because we only investigated the patterns in elevation range from 0 to 600 m (0 to 2,000 feet). Furthermore, different phases may affect alpha diversity of a state. For example, the litter phase of annual grass state is much lower in alpha diversity than the lupine and annual grasses and forbs phase. For this reason, measuring plant diversity for multiple years is important to capture the range in alpha diversity of each ecological site.

Similar to Casado et al.,<sup>15</sup> we found that grasslands were more species diverse and more even than shrublands, but when we accounted for the size of grasses and shrubs, we found that the difference in species richness in these vegetation states were not significant across ecological sites. This result is not surprising because the grasslands and understory of shrubs were dominated by non-native, annual grasses. Species that filled the understory niches were ripgut brome, red brome and wild oat which are all strong resource competitors, limiting the growth of other species.<sup>35</sup> In general, the presence of shrubs in semi-arid grasslands enriches the soil as shrubs translocate resources underneath their canopy,<sup>36</sup> promoting species that are competitive in high resource environments to occupy the area.<sup>37</sup>

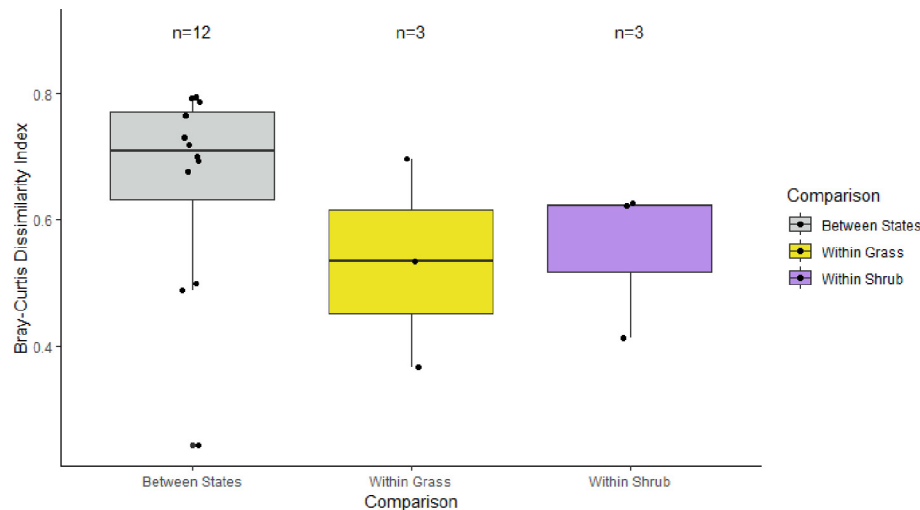
Unsurprisingly, there was high compositional turnover between grasses and forbs, and a mosaic of grasses and forbs lead to high diversity. We found that beta diversity was higher between grassland and shrubland states than within each state across sites, which means the presence of shrubs can change the understory grass community. Shrubland states contribute



**Figure 6.** Rarefaction curves for the San Joaquin Valley Holocene Flats (shown in blue), Lower Miocene Hills (shown in purple), and Upper Miocene Hills (shown in red) on Tejon Ranch, Kern County, California. Solid lines indicate shrub plots and dashed lines indicate grass plots. Vertical lines indicate the smallest number of observations.



**Figure 7.** Functional diversity similarity across ecological sites. Proportion of **A**, native annual forbs; **B**, native annual grass; **C**, native perennial forbs; and **D**, native perennial shrubs in grasslands (yellow) and shrublands (purple). Any two means sharing a letter are not statistically different using the Tukey test. The boxplot indicates the median (center line), the first and third quartiles (box), and distant quartiles (whiskers). The sample size was 48 (12 plots  $\times$  4 transects per plot). Holo indicates San Joaquin Valley Holocene Flats ecological site; LowMio, Lower Miocene Hills ecological site; UpMio, Upper Miocene Hills ecological site.



**Figure 8.** Turnover in community structure (i.e., beta diversity) measured by Bray-Curtis Dissimilarity Index between grassland (yellow) and shrubland (purple) states were significantly higher than that within states. Higher values of the Bray-Curtis Dissimilarity Index indicate greater dissimilarity in species composition. All pair-wise comparisons were made within each ecological site. The boxplot indicates the median (center line), the first and third quartiles (box), and distant quantiles (whiskers). Points are raw data.

to unique aspects of diversity not present in the grassland states. For example, native shrubs in this region provide habitat for other species, such as the endangered blunt-nosed leopard lizard (*Gambelia sila*),<sup>38</sup> and nectar for pollinators. The ESD-STM framework enables managers to focus their conservation efforts for targeted species on a specific site.

To achieve Tejon Ranch's goal of maintaining heterogeneity at the landscape level, management of both shrubland and grassland states is needed. Restoration from annual grassland states to native shrubland state (T5 in Fig. 3) is possible by planting native shrubs in a wet year.<sup>39</sup> Where to plant these shrubs on the landscape depends on the trade-off between the conservation and livestock management goals. In our study, for example, planting saltbush in either Holocene Hills or Lower Miocene Hills Ecological Sites would yield the same outcome for biodiversity, but planting saltbush in Lower Miocene Hills—in less productive grassland—would leave more forage for livestock (Fig. 3). This is how the ESD-STM framework could be used to achieve multiple optima.

## Implications

Many range managers aim to manage for multiple goals, but there has not been a sufficient tool for it. We demonstrated that the ESD-STM framework could be expanded beyond species composition to prioritize areas for species and functional diversity conservation in addition to livestock production on a heterogeneous landscape. This is especially valuable in managing shrub-grass mosaic ecological sites, where shrubland states and grassland states have trade-offs between forage and species and functional diversity. The definition of biodiversity can be different depending on what goals managers want to achieve, but the ESD-STM framework is flexible for comparing multiple diversity metrics.

## Declarations of interest

None.

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