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RESTORATION MANAGEMENT FOR SPATIALLY AND TEMPORALLY COMPLEX CALIFORNIAN GRASSLAND

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ABSTRACT

Introduced species from the Mediterranean dominate plant cover of the Californian grassland, but more than one thousand native species persist at low abundance or may be locally absent. Efforts to successfully increase native abundance are complicated by the spatial and temporal complexity of the system. Highly variable rainfall, topography, and soils result in large differences in species composition across space and time. Managers must deal with this variability to carry out effective restoration. We present a conceptual management toolkit containing five steps to better organize variability, predict suitable restoration sites, and select and time treatments. The toolkit relies on the key concepts of ecological site classification, state-and-transition models, and opportunistic adaptive management to help managers achieve their restoration goals.

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INTRODUCTION

California's grassy hills and plains have long captured imaginations with their beauty and promise of economic opportunity. These grasslands provide forage for livestock and wildlife (Jackson & Bartolome 2007), habitat for 40% of the state's native plant species (Schiffman 2007), and carbon sequestration (Booker et al. 2013). Despite the ecosystem services they provide, grasslands are among the most fragmented and developed natural systems in California (Jantz et al. 2007). A dramatic invasion of species from the Old World has also greatly impacted Californian grassland. Restoration must address historical sources of degradation (e.g. species invasion, past cultivation) along with new ones (e.g. fragmentation due to increasing urbanization; FRAP 2010).

Managers are grappling with the critical decision of how to best allocate their restoration resources; here we argue that the spatial and temporal variability of these grasslands should be a central consideration in the decision-making process (Landres et al. 1999; Bartolome et al. 2009; McBride et al. 2010). We present a conceptual toolkit that can help managers understand the variability and incorporate their understanding into restoration management. We begin by outlining the drivers of grassland species composition, using examples from central and southern California. Next we describe some of the restoration constraints of this system. We then present the five-step toolkit, first by explaining its conceptual framework and second by outlining step-by-step instructions for its use. We conclude with a case study describing the application of the toolkit in southern California. While our focus is on California's Mediterranean-climate grasslands, this toolkit can be applied to other terrestrial ecosystems with high spatial and temporal variability across the state and world.

Controls over Species Composition in Californian Grassland

The Californian grassland discontinuously covers about 11% of the state (Davis et al. 1998), spanning a significant precipitation gradient and a variety of topographic and edaphic features (Huenneke 1989). This extensive spatial distribution contributes to regional differences in species composition, and three major grassland types have been identified: Coastal Prairie, Coast Range Grassland, and Valley Grassland (see Barbour et al. 2007; Jackson & Bartolome 2002 for more detailed information). Here we focus on the drivers of community composition within Valley Grassland, the most extensive grassland type in California.

The majority of Valley Grassland sits on the alluvium and foothills on the edges of California's Great Central Valley, a sediment basin circumscribed by the Sierra Nevada to the east and the California coast ranges to the west (Figure 1; Heady 1977; Heady et al. 1991). Valley grasslands are in California's Mediterranean climate zone of hot dry summers and wet cool winters. Like grasslands in other Mediterranean climate zones worldwide (Dallman 1998), valley grasslands are dominated by annual species. The most abundant valley grassland annuals, however, are not native to California. A widespread type conversion from native species to Mediterranean species occurred in the nineteenth century (Jackson 1985; Baker 1989). A handful of exotic annual species are the overall dominants; however, native species, especially native annual forbs, often contribute to the high species richness found in

valley grasslands (Gennet 2007; Fernandez-Going et al. 2012). Also, though they are relatively rare, valley grasslands with extensive native communities still exist (Kimball & Schiffman 2003; Lulow & Young 2011).

Valley grasslands span a regional-scale latitudinal climatic gradient, from the wetter north to the drier south. This north-south gradient is modified by the rain shadow of the coast ranges, with the coastal foothills and valleys in the west more mesic than the xeric interior Central Valley and Sierra Nevada foothills to the east. The longitudinal precipitation gradient is reflected in a parallel gradient in species composition in which perennial bunchgrasses are more common in the more mesic valley grasslands nearer to the coast and less common in the

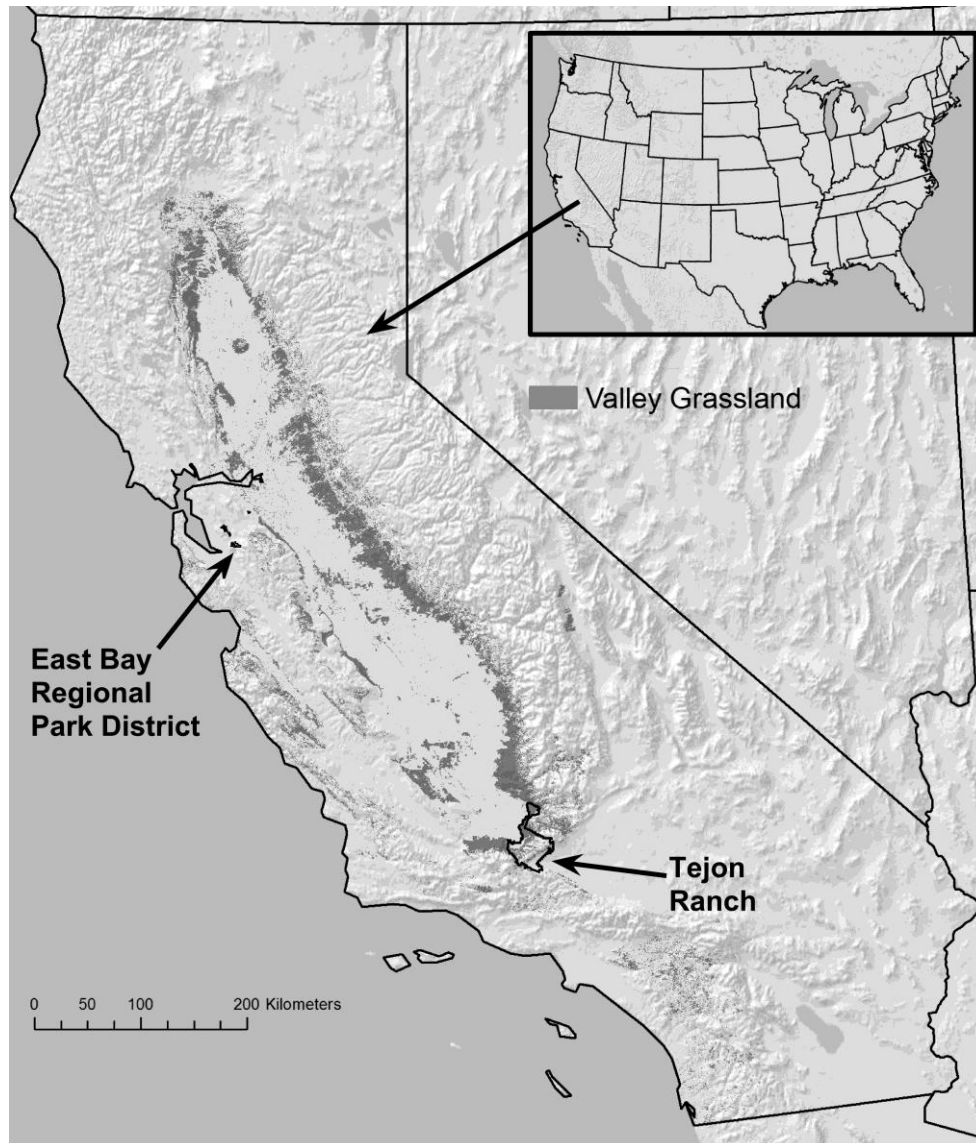


Figure 1. Distribution of the Valley Grassland vegetation type in California, USA (USFS 2010). The managed landscapes featured in the two case studies, the East Bay Regional Park District and Tejon Ranch, are also shown.

xeric interior valley grasslands (Burcham 1975; Heady 1977; Bartolome et al. 2007a).

In addition to this spatial variation, the climate of valley grasslands also varies temporally: intra-annually due to the Mediterranean seasons, and inter-annually due to largely stochastic rainfall timing and amount. In a recent data synthesis, Hallett et al. (*in press*) found that compared to more mesic grasslands like the tall grass prairie in Kansas or old fields in Michigan, California grasslands have greater inter-annual precipitation variability. The coefficient of variation of annual precipitation is 20-25 in Kansas and Michigan but 31-37 in California. This temporal variation results in strong inter- and intra-annual differences in species composition (Heady 1958; Pitt & Heady 1978; Bartolome 1989). A classic example of how this temporal variation affects species composition is “grass” vs. “filaree” years. After the initial germinating rains of a given year, a period of drought is associated with a higher abundance of filaree (*Erodium* spp.), while frequent precipitation after the initial rains results in a higher abundance of annual grasses like wild oats (*Avena fatua*) and soft chess (*Bromus hordeaceus*). The degree of temporal variability of species composition at a site is modified by the site’s productivity, topography, and soils (Bartolome et al. 2007b; Gennet 2007; Fernandez-Going et al. 2012).

Within zones of a singular climate, topographic and soil properties such as elevation, slope, and soil type are fundamental controls on valley grassland species distribution (Burcham 1975; Evans et al. 1975; Evans & Young 1989; Eviner & Firestone 2007). This control was apparently in place in the past, as well. For instance, there is strong evidence that before the major invasion of exotic species, when annual forbs were more extensive than grasses (Schiffman 2007; Minnich 2008), grasses were restricted to sites like stream terraces (Evet & Bartolome 2013).

Contrasting findings on the particular soil nutrients that control species abundance and distribution in valley grasslands underscore the need to consider spatial heterogeneity when conducting restoration. For example, there is a general trend that lower fertility sites are more likely to support native perennial bunchgrasses, but the roles of specific nutrients can vary among sites in a landscape. In the highly invaded valley grasslands of the Diablo Range of central California, for instance, one study documented that low-nitrogen sites support the native perennial bunchgrass *Stipa pulchra* (Robertson 2004), whereas another study in neighboring grasslands found that the species is more often found in low-phosphorus sites (Gea-Izquierdo et al. 2007).

A useful concept for understanding controls on species composition in rangelands (grasslands, shrublands, savannas) is a theoretical continuum with equilibrium and non-equilibrium community models at its extremes (Wiens 1984; Vetter 2005). In equilibrium models, dominant controls over the structure and function of communities are biotic interactions like plant competition and herbivory. In contrast, in non-equilibrium models, communities are structured more by external factors such as climate (Wiens 1984; Ellis & Swift 1988), topography (Milchunas et al. 1989), and abiotic soil properties (Booker et al. 2012). The spatial scale at which rangeland is observed affects whether equilibrium or non-equilibrium dynamics are detected (Wiens 1989), but there is a general trend that rangelands with highly variable abiotic environments are best described using non-equilibrium models (Ellis & Swift 1988; Briske et al. 2003). A working hypothesis is that non-equilibrium models are appropriate for rangelands with a coefficient of variation of inter-annual rainfall exceeding 33 (von Wehrden et al. 2012).

As one might expect given their variability, including their high coefficient of variation of inter-annual rainfall, California's valley grasslands exhibit non-equilibrium dynamics on multiple spatial scales (Jackson & Bartolome 2002). Biotic interactions (e.g. cattle grazing, plant litter on germinating seeds) certainly affect community dynamics (Huntsinger et al. 2007), but overall, abiotic factors appear to be stronger controls (Jackson & Bartolome 2007). Californian grassland can also be strongly affected by long term processes that cannot be categorized as biotic or abiotic, such as altered fire regimes, novel species invasions, and anthropogenic nitrogen enrichment. Establishing the system's placement on the theoretical continuum from equilibrium to non-equilibrium can help managers make predictions about the impacts of these processes.

CASE STUDY 1: SPATIAL AND TEMPORAL VARIATION IN VALLEY GRASSLAND

To illustrate spatial and temporal species composition dynamics, we present data from valley grasslands managed by the East Bay Regional Park District (EBRPD) and the Tejon Ranch Conservancy (Tejon). EBRPD grasslands lie in the Diablo Range east of San Francisco, California. The Tejon Ranch, a vestige of the Mexican-California Rancho land ownership system, spans 1093 km² (Figure 1). It is the largest privately owned contiguous property in California. The EBRPD and Tejon grasslands are largely dominated by naturalized exotic annual grasses but maintain high native species richness (Gennet 2007). At Tejon, native grassland communities are extensive on some sites (see Case Study 2).

Here we compare grasslands at three EBRPD regional parks (Pleasanton Ridge Regional Park, Sunol Regional Wilderness-Ohlone Regional Wilderness, and Vasco Caves Regional Preserve) with grasslands of the northern half of Tejon Ranch. Tejon's northern grasslands cover 22,000 ha on four distinct geophysical areas: the San Joaquin Valley (the southern portion of the Great Central Valley, SJV), southernmost Sierra Nevada mountains (SN), Tejon Hills (TH), and Tehachapi Mountains (TM).

In order to guide long term management efforts, grasslands at EBRPD and Tejon were sampled for species composition over multiple years, 2005-2012 at EBRPD and 2010-2012 at Tejon. At EBRPD, six 500 m² circular plots were sampled at each park. Within each plot, four 17 m transects were laid in the cardinal directions and identity of the first species hit by a dropped pin was recorded every 0.5 m along each transect. At Tejon, different numbers of plots were sampled in each geophysical area (SJV n = 9, SN n = 3, TH n = 8, TM n = 9). Like the plots at EBRPD, the plots at Tejon comprised four transects, each pointing in a cardinal direction, and the first species hit by a dropped pin was recorded every 0.5 m on each transect. Tejon plots are larger than EBRPD plots, with 25 m transects instead of 17 m transects. All plots at Tejon and EBRPD were lightly to moderately grazed by cattle or sheep (~0.4 Animal Unit Months/ha; McDougald et al. 1991) throughout sampling, except for three plots in Pleasanton Ridge Regional Park that were not grazed for two years.

Figure 2 shows the precipitation (Figure 2a), species richness (Figure 2b), and temporal and spatial beta-diversity (Figure 2c) of EBRPD and Tejon. The precipitation curves represent the average of the precipitation recorded at each EBRPD park and each Tejon geophysical area. The species richness and beta-diversity curves (Figures 2b and 2c,

respectively) represent twice-averaged values. First, plot values were averaged within each park and geophysical area to yield park-scale and geophysical area-scale values. Second, the park-scale values were averaged together to yield EBRPD landscape-scale values (circles) and the geophysical area-scale values were averaged together to yield Tejon landscape-scale values (squares).

Precipitation differed between the EBRPD and Tejon landscapes in 2010-2012 (Figure 2a); however, both typically experience high variability in inter-annual rainfall (PRISM Climate Group 2013). This variability supports the working hypothesis that these grasslands should be placed on the non-equilibrium end of the theoretical continuum discussed above.

Species richness of the two landscapes is similar (Figure 2b). It fluctuated slightly over time in EBRPD and decreased in 2011 for both EBRPD and Tejon when precipitation was high.

In addition to changes in species richness, variation in species composition can also be measured as the turnover of species (beta-diversity) in a plot from one year to the next or among plots within any given year (Whittaker 1960, Anderson et al. 2006). We used a dissimilarity metric (Bray-Curtis), in which values range from 0 (similar) to 1 (dissimilar), to estimate beta-diversity. This analysis revealed that the variation in community structure differs slightly between EBRPD and Tejon, with Tejon having greater turnover (Figure 2c). The variation of the two landscapes, however, fluctuated similarly over time (i.e. the Tejon and EBRPD curves track each other from 2010-2012). The slight increase in temporal variability in species composition between 2010 and 2011 in both landscapes likely reflects changes in composition that resulted from the high rainfall across California in 2011. Temporal turnover (open symbols) was lower compared to spatial turnover (filled symbols) suggesting that community structure changes less from one year to the next at a given plot than it does from one plot to the next in a given year. This temporal similarity in species composition supports the previously observed pattern of temporal nestedness within California grasslands, where interannual rainfall patterns similarly influence most species within a community (Elmendorf & Harrison 2009).

Variability in species composition among plots at EBRPD and Tejon was relatively consistent over the years (filled symbols, Figure 2c), suggesting that the site-specific constraints on species composition are maintained over time. Strong site effects on species abundance patterns were also observed for EBRPD by Gea-Izquierdo et al. (2007), who found that the abundance of *Stipa pulchra* was strongly regulated by the phosphorus levels and sand content of the soil. Both Gea-Izquierdo et al. (2007) and Gennet (2007) found minimal impacts of livestock grazing on vegetation structure in EBRPD.

The range of spatial variability in species composition observed in these grasslands (0.5-0.7) is similar to that which has been observed in grasslands in other dry climates. Using a similar dissimilarity metric (Jaccard's), Chalcraft et al. (2004) found that a xeric grassland in southern New Mexico had variation in community structure that ranged from 0.4-0.75 compared to a mesic grassland in northeastern Kansas where variability did not exceed 0.45.

Teasing apart the effects of temporal and spatial variability on species composition is an important consideration when developing management strategies for Californian grassland. At the central and southern California valley grasslands showcased here, species composition varied more strongly across space within each managed landscape than it did across time. This finding reveals the strong influence that site conditions have on species composition. Accordingly, site conditions should be strongly considered during restoration planning.

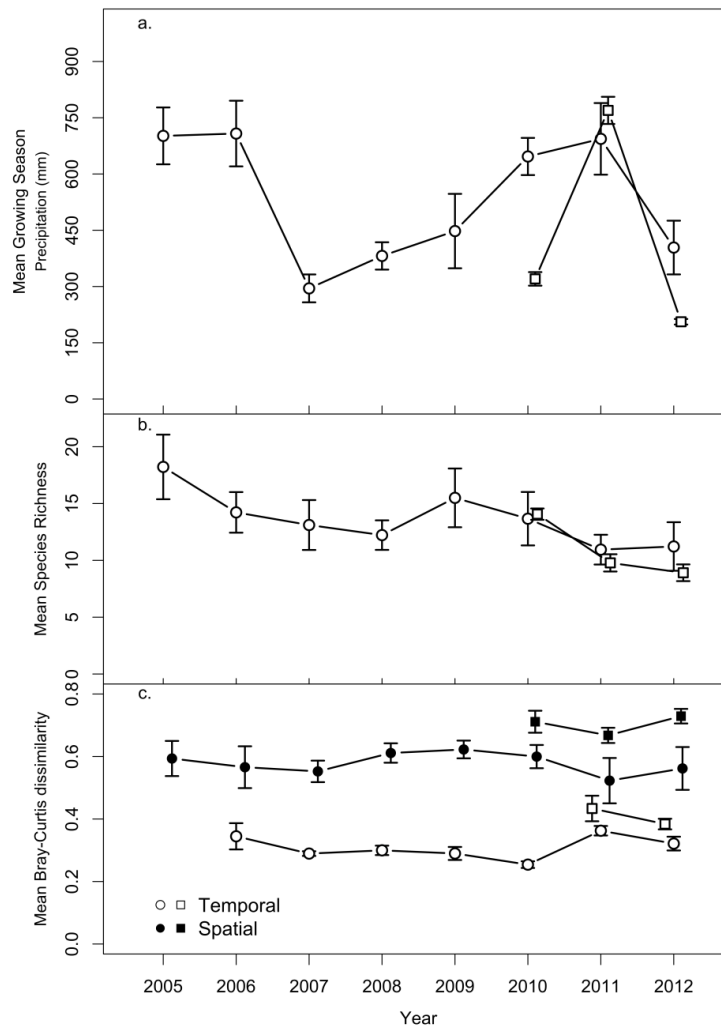


Figure 2. Mean growing season precipitation (a), species richness (b), and temporal and spatial beta-diversity (c) in the valley grasslands of the East Bay Regional Park District (circles) and Tejon Ranch (squares). Growing season precipitation was defined as rainfall from October to June (e.g. 2006 growing season was from October 2005 to June 2006). EBRPD species richness and beta-diversity curves represent values from 18 plots across 3 parks, averaged within and then across the parks. Tejon species richness and beta-diversity curves represent values from 30 plots across 4 geophysical areas, averaged within and then across the geophysical areas. Species richness was estimated as the total number of unique species hit along four transects in each sampling plot. Temporal beta-diversity is estimated as the pairwise comparison of the previous and current year species composition of a plot. Spatial beta-diversity is estimated as the mean pairwise difference in species composition of the plots sampled in a given year. Precipitation data for three EBRPD parks was downloaded from the nearest weather stations of California Department of Water Resources and any missing data was supplemented by weather stations from California Irrigation Management Information Services; precipitation data for four Tejon geophysical areas was downloaded from PRISM (PRISM Climate Group 2013). Error bars represent ± 1 standard error.

Management of Californian Grassland

Grassland restoration in California typically involves reducing the abundance of exotics while increasing the abundance of natives (Seabloom et al. 2003a; Bartolome et al. 2004; Stromberg et al. 2007; Lulow 2008), but completely eradicating the naturalized exotic species is usually not feasible (Bartolome et al. 2007a). Many restoration projects are geared toward re-introducing or augmenting populations of native perennial bunchgrasses using agronomic methods (Stromberg et al. 2007). Livestock is the major economic product of the Californian grassland, and though restoration is largely the domain of conservation organizations, public agencies, and land trusts, common objectives of livestock operators can be synergistic with objectives of restoration managers. Such objectives include increasing forage productivity, improving soil stability, and providing wildlife habitat (Huntsinger et al. 2007).

Restoration efforts have been met with mixed success (Stromberg et al. 2007; D'Antonio et al. 2002). A vexing problem for assessing the success of any California grassland restoration effort is that the original vegetation is relatively unknown, resulting in the lack of a suitable reference system (Bartolome et al. 2009). Restoration success is also thwarted by the inability to replicate management efforts across California due to the strong effects of spatial and temporal variability on vegetation structure and productivity (Bartolome et al. 2007b & 2009; Wilson et al. 2011) as well as the variability of past human activity among sites (Stromberg & Griffin 1996; Hamilton et al. 2002).

Land use legacies, invasive species, and biotic interactions may significantly impede efforts to re-establish native species (Stromberg & Griffin 1996; Orrock et al. 2008). Old fields experienced large-scale soil disturbances such as plowing and disking that permanently altered soil structure and soil microbial communities (Steenwerth et al. 2002), creating dynamics that favor exotics (Stromberg & Griffin 1996). Invasive species are major obstacles to grassland restoration in California. Long-term invader dominance of an area can greatly reduce the native seed bank, preventing native recovery even once the invader has been removed (Cox & Allen 2002; Seastedt et al. 2008). Additionally, some invaders create soil legacies by altering the soil biota, releasing allelopathic chemicals, or creating litter that detrimentally affects native recruitment (Hawkes et al. 2005; Reinhart & Callaway 2006; Vogelsang & Bever 2009). The small mammals of Californian grasslands can also thwart native recovery. Gopher activity can often favor exotic annual grasses (Hobbs & Mooney 1995; Stromberg & Griffin 1996; Seabloom 2003b) and preferential seed predation of native species can also limit the success of restoration management (Orrock et al. 2009). Understanding the degree to which these factors constrain recovery can guide the selection of management treatments.

Another recovery constraint is financial. Improving the efficacy of restoration management requires descriptive and predictive models that can account for the spatial and temporal dynamics of vegetation as well as any potential site-specific recovery constraints (Hobbs 2007; Bartolome et al. 2009; Suding & Hobbs 2009). The science-based toolkit we present in the next section requires a site-specific and data-intensive approach, which can be time-consuming and therefore expensive. We contend, however, that while the cost of a science-based approach is high, it reduces the uncertainty that inevitably complicates Californian grassland restoration planning (McBride et al. 2010; Wilson et al. 2011). More certainty should translate into better chances for using limited financial resources on successfully achieving restoration objectives (Landres et al. 1999).

A Management Toolkit for Spatially and Temporally Complex Grassland

The variability and restoration constraints outlined above can be daunting obstacles to the conservation and enhancement of native vegetation in California's valley grasslands. One response to these obstacles is a heavy-handed approach, in which natives, often perennial bunchgrass species, are cultivated using agronomic methods to overcome potential constraints imposed by soils or rainfall signatures (Stromberg et al. 2007). We suggest an alternative approach in which spatiotemporal variability is actively embraced (Eviner & Hawkes 2008) and used as a guide in restoration planning (Landres et al. 1999), to match species palettes and restoration techniques with suitable sites and auspicious timing (White & Walker 1997). This alternative approach is a science-based strategy founded on ecological site, state-and-transition, and auxiliary models and is appropriate in a framework of adaptive and opportunistic management. Our approach is appropriate for managers with extensive land and multiple conservation goals but limited funding — a common scenario in California's valley grasslands (Huntsinger et al. 2007).

Ecological site and state-and-transition models are useful tools for describing and understanding terrestrial landscapes with high spatiotemporal variability. These conceptual tools are important elements of our five-step toolkit (Figure 3). An ecological site is an assemblage of landscape units, or sites, that have the same potential vegetation and respond similarly to management (Bestelmeyer et al. 2009). The basic idea that geologic, topographic, and soil (topo-edaphic) properties are the primary governing agents of a site's potential vegetation and response to management is increasingly accepted for terrestrial landscapes, having been verified through observation and manipulative experimentation (Grigal et al. 1999; Bestelmeyer et al. 2009; Brown 2010). Accordingly, the sites in ecological site classifications are best defined by their topo-edaphic properties (Bestelmeyer et al. 2009). Given the strong influence of abiotic factors on vegetation dynamics in non-equilibrium systems, topo-edaphic control of site potential may be especially applicable to these systems (Booker et al. 2012). The sites constituting an ecological site are not necessarily contiguous, but instead are typically arrayed across the landscape in a mosaic pattern (Bestelmeyer et al. 2009). The sites are irregularly sized, but they are larger than plot or patch and smaller than landscape, at approximately 5-50 ha (10^4 - 10^5 m²; Bestelmeyer et al. 2011a).

A state-and-transition model is a description of the spatial (Bestelmeyer et al. 2011b) or temporal vegetation change at an ecological site, in which a change from one vegetative state to another is called a transition (Westoby et al. 1989). By pairing each ecological site with a state-and-transition model, the grassland manager can understand the vegetation dynamics occurring on that ecological site. This understanding can help the manager predict future dynamics and select suitable management objectives and tactics for the ecological site (Herrick et al. 2006; Bestelmeyer et al. 2009).

The theory underlying ecological site and state-and-transition modeling has important implications for restoration. An ecological site can contain reference areas with desirable states as well as degraded areas with undesirable states. The reference and degraded areas are part of the same ecological site, so they theoretically have the same potential vegetation. As a result, the management team can have some certainty that restoration treatments on the degraded areas can foster transitions to the desirable states seen on the reference areas (White and Walker 1997; Bestelmeyer et al. 2011b).

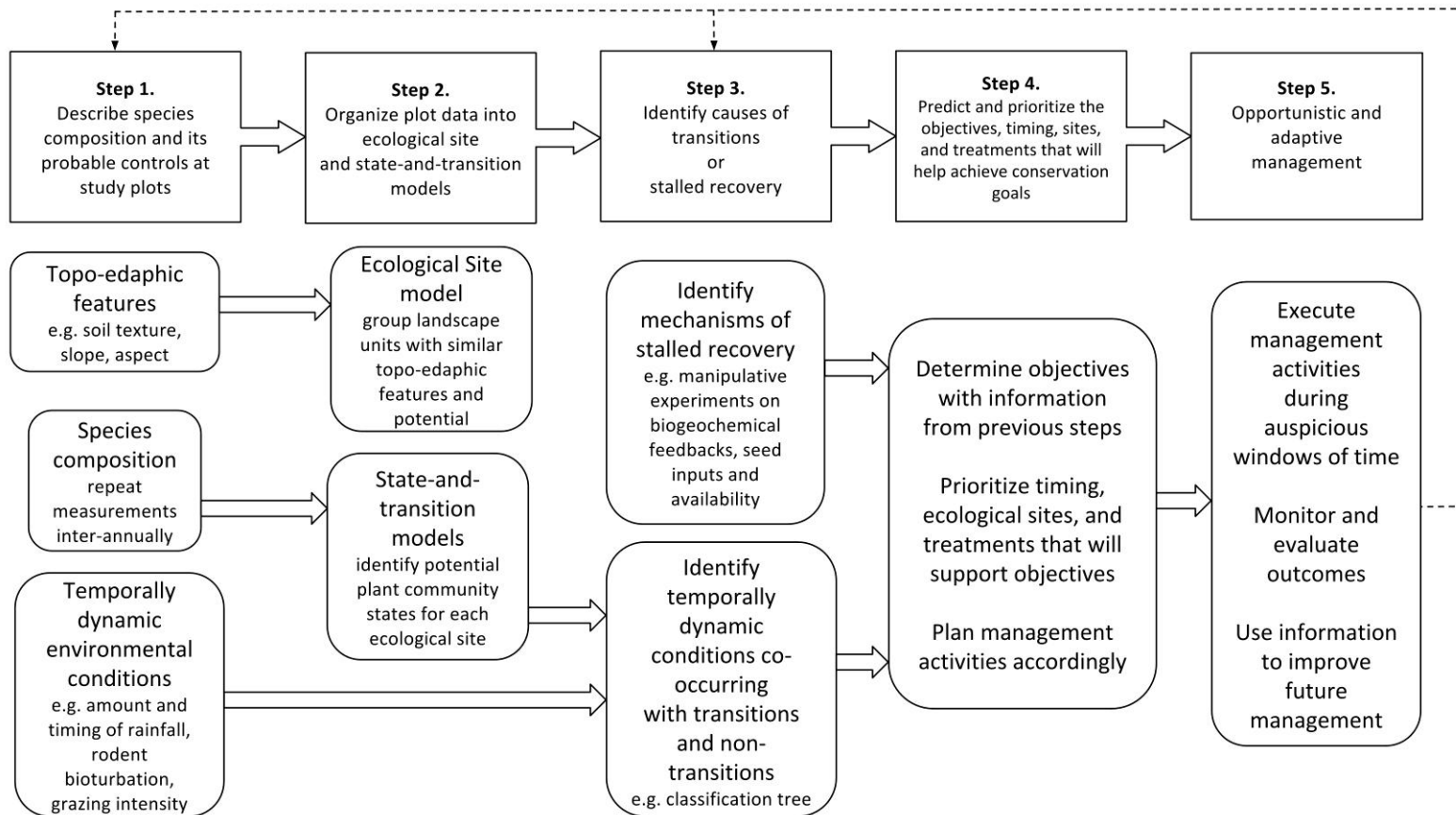


Figure 3. Framework of the management toolkit for spatially and temporally complex grassland. Tools in the steps help managers describe and understand the variation of the managed landscape and use their understanding to guide management decisions. The dashed arrow represents the adaptation of understanding about the landscape (developed in Steps 1-3), which may be necessary if monitoring indicates that the execution of management activities (Step 5) did not achieve objectives (defined in Step 4).

Due to the demonstrated utility of ecological sites and state-and-transition models, United States (U.S.) land management agencies have formally adopted their use and have specified official protocols for their creation (Caudle et al. 2013). Our approach to building and presenting these models differs from the government's in a few ways, which we describe in our explanation of Step 2, below.

An assumption underlying the toolkit is that the management team will specify conservation and restoration goals before taking any of the toolkit steps. Goal setting is especially important when multiple stakeholders are involved. Because goals, which represent a future desired state or condition, are often general or idealistic, they should be paired with specific and practical objectives that specify how the goals will be achieved (Bush 2006). In Step 4, management teams will use their understanding gleaned from Steps 1-3 to specify objectives and determine the tactics that will support the realization of those objectives. The plans made in Step 4 will be executed in Step 5, opportunistic and adaptive management. Pairing adaptive management (Holling 1978) with opportunistic management (Westoby et al. 1989) can translate into higher chances of achieving conservation goals in terrestrial systems with high spatiotemporal variation.

A second assumption is that a science-based approach – in which ecosystem description leads to an understanding that can inform sound predictions and ultimately enhance the ability to control the ecosystem (Begon et al. 1996; Bartolome et al. 2009) – is more effective than a non-scientific approach. We refer the reader to a complementary framework for science-based management of rangelands put forth by Herrick and others (2006), who advise that management teams define the ecological potential of, and management strategies for, an ecosystem using ecological site and state-and-transition models; assess the functional status of the ecosystem with respect to its potential; and monitor how that functional status changes over time with and without management inputs (Herrick et al. 2006; Karl & Herrick 2010). Sheley and others (2010) also offer a framework for model-based management of rangelands, with a focus on invasive plants. While our understanding of rangelands has been improved by the work of these colleagues, our framework differs from theirs. Next we describe the tools of our toolkit as a series of five steps that evolve from description to understanding to prediction to control.

Step 1 - Describe species composition and its probable controls at study plots

The models in Steps 2 and 3 that form the backbone of the toolkit are built upon plot-based measurements of topo-edaphic features, species composition, and temporally-dynamic environmental conditions. Using hierarchy theory, we make the assumption that linkages between the environment and species observed at 10^2 to 10^3 m² study plots also occur at the extent of the 10^4 to 10^5 m² sites that constitute an ecological site. We assume this ability to scale up is strengthened by randomly siting plots but stratifying them across multiple zones in order to embody gradients in topography, soil properties, and vegetation “nativeness”. Sampling the plots repeatedly through time should also help justify scaling up (Bartolome et al. 2009).

Random sampling may not be appropriate for all projects. For example, if the management goal is the restoration of a single species (e.g. increase abundance and distribution of *Stipa pulchra*), investigators may prefer to measure ecosystem characteristics only in areas known to support that single species. For goals that are not tied to particular species but instead represent broader ideals such as “enhancing native biodiversity,” random

sampling can protect management teams from reliance on preconceived notions about restoration potential that tend to be strengthened by subjectively placing plots only in areas that reinforce those preconceived notions.

Within a valley grassland of uniform climate, we predict that topo-edaphic characteristics will be the principal controls on plant community structure, and accordingly, we recommend the ecological site classification model in Step 2 be populated with topo-edaphic data. Deciding the particular topo-edaphic features to measure is a site-specific process, with local expertise the best guide. In valley grasslands, ideal sampling would cover the chemistry, texture, and depth of the soils as well as the factors that impact soil formation, such as slope, aspect, climate, and site history (Jenny 1941). When site history cannot be reconstructed, empirical soil characteristics can act as proxies (Steenwerth et al. 2002). Because many soil properties change diurnally, seasonally, annually, or on longer timescales, site-specific considerations must dictate whether one-time sampling of topo-edaphic properties is sufficient for the ecological site model (Grigal et al. 1999).

Sampling the entire soil profile will reveal information about depth trends, pedogenesis, and taxonomic classification of the soil (Brady & Weil 2002; Soil Survey Staff 2010), but we recommend that sampling depth be determined by the rooting depths of the majority of the extant and target species. We predict that for California grasslands, in which most plants have the majority of roots at 60 cm or shallower (Holmes & Rice 1996; Hunter & Wu 2005), assaying soil taken from a sub-meter depth and measuring depth to restrictive layer is sufficient to understand the most informative plant-soil relationships.

Deciphering how strongly the topo-edaphic properties being measured are structuring the plant community can indicate whether an ecological site classification based on those properties will, in fact, efficaciously inform predictions. A modeling technique useful for this purpose is BIO-ENV (Clarke & Ainsworth 1993), which relates community and environmental data by correlating community structure with each possible combination of environmental variables. Model output provides a list of correlations, which offers a sense of how well the full set of environmental variables explains community structure, as well as which environmental variables best explain community structure.

A correlation lower than 0.3 between the species and the “best” subset of topo-edaphic variables is unexpected in non-equilibrium ecosystems. A management team faced with such a low correlation may elect to sample a different set of topo-edaphic factors. Alternatively, they may conclude that defining site potential using topo-edaphic properties is not appropriate and may classify landscape units using recovery constraints such as land use legacies and invasive species (the toolkit does not cover this approach). The BIO-ENV modeling exercise is also useful for streamlining future sampling efforts. Because the variables that are not part of the “best” subset may be redundant, they can be omitted from future sampling with some certainty that no critical information will be lost.

Repeatedly measuring species composition at numerous plots, though expensive, would allow the management team to build temporal state-and-transition models. The transitions in such data-driven models would symbolize inter-annual changes observed during the study; however, we hypothesize that these would be predictive with respect to inter-annual as well as decadal time scales. In valley grasslands with few perennials, three or more inter-annual samples of species composition taken during springtime peak growing season can inform predictive state-and-transition models. Systems with extensive perennials may require more sampling years than a system dominated by annuals.

Measuring temporally-dynamic environmental conditions concurrently with replicated species composition samples allows the management team to isolate the temporal conditions associated with plant community transitions and stalled recovery. Determining the suite of potential influences on temporal species composition dynamics is ultimately a local process, but likely factors in valley grasslands include weather (e.g. monthly rainfall totals, Julian date of first significant rainfall, monthly average coldest temperature), seedbank dynamics, herbivory and disturbance by livestock and wildlife, and plant litter. Measuring some potential influences on species composition in the spring and then other potential influences in the fall when only residual dry vegetative matter (RDM) remains can be instructive (Heady 1956; Bartolome et al. 2002). Isolating the set of variables may be best achieved through small-scale experiments, such as livestock grazing trials with paired grazed and ungrazed plots (Kettenring & Adams 2011).

Step 2 - Organize plot data into ecological site and state-and-transition models

If the management team is satisfied with the correlation of species composition and environmental properties measured, they can proceed to Step 2: using the data to build ecological site and state-and-transition models. The models are analytically straightforward, but local, objective expertise is critical to interpreting the models and communicating results to stakeholders.

The ecological site model is borne out of describing and understanding the topographic and edaphic environment of the focal area. Once decisions have been made about the set of variables to measure and data have been collected at the plots (Step 1), hierarchical cluster analysis can parse the plots into ecological site groupings. Several auxiliary analyses are available to ensure accurate and unbiased pruning of the cluster dendrogram (e.g. Mantel test; Borcard et al. 2011); to identify the key variables that are differentiating the clusters (e.g. conditional box plots; Verfaillie et al. 2009); and to verify that the clusters are statistically significantly different from each other with respect to the key variables (e.g. non-parametric Kruskal-Wallis test for differences between groups; Whitlock & Schluter 2009). Local decisions should be made about whether all plots in the topo-edaphic dataset should be included in a global cluster analysis, or whether plots should be modeled in separate groups. A possible reason for splitting the plots *a priori* would be a distinct climatic difference among two groups of plots that is recognized by stakeholders but would not be recognized by a global cluster analysis.

For managers to effectively use ecological site classifications, they need the ability to stand in any area of the management landscape and determine its ecological site. Managers adopting our approach can approximate the ecological site class of an area by consulting geology and soils maps; using visual cues of topography and elevation; and informally determining surface soil texture. In order to absolutely verify that the soil of the area falls within the ecological site, the manager must determine depth to restrictive layer and assay soil taken from a depth of 15 to 60 cm, to be determined by management goals. They would not be required to identify diagnostic soil horizons to taxonomically classify the soil.

If the budget allows, we recommend replicating species composition data collection inter-annually to build a state-and-transition model for each ecological site. A cluster analysis and/or ordination on the community data matrix (McCune & Grace 2002; Borcard et al. 2011) can reveal states and transitions. For this type of analysis, we create a community data matrix with each row representing a particular plot's species during a particular sampling year

(hereafter “plot × year”). Transitions are detected by the plots’ movement through ordination or cluster space. For example, if a particular study plot (“Plot A”), for a particular year (“Plot A × 2007”), is in a cluster with plot × years dominated by native annual forbs, but for a subsequent year, the plot (“Plot A × 2009”) is in a cluster with plot × years dominated by exotic annual grass, a transition has occurred. It is critical to demarcate ordination groupings and prune cluster diagrams objectively. Indicator Species Analysis, which isolates the species that are driving the differences between the cluster groupings (Dufrene & Legendre 1997), can be used for this purpose when used in concert with a randomization procedure (McCune & Grace 2002).

Statistical analyses for the state-and-transition and ecological site models may not be sensitive enough to pick up dynamics that are observed on the ground, and it may be necessary to alter model results *a posteriori*. Such alterations may include assigning a study plot to a different ecological site or re-assigning plots to an extra state that is known to occur on the ecological site and is important to stakeholders, but that was non-existent during sampling. In addition, if a conservation objective is enhancing a particular functional group (e.g. native annual forb, native perennial bunchgrass), the management team may choose to lump the species composition clusters into states defined by functional groups. Similarly, the team may lump multiple site clusters into a single ecological site. A general rule of thumb when altering the models *a posteriori* is remaining as objective as possible and favoring empirical information instead of preconceived notions.

Presenting the models clearly will be critical to communication among stakeholders. State-and-transition models are commonly presented as box and arrow diagrams showing states and transitions, with a catalogue of states and a catalogue of transitions that includes hypotheses about why the transitions occurred (Westoby et al. 1989). Ecological sites can be displayed with stylized diagrams (see Case Study 2) or maps with plot symbols color-coded to represent the ecological site groupings. Ecological site names that incorporate the local vernacular can help facilitate communication.

As mentioned above, three U.S. government land management agencies formally adopted ecological site and state-and-transition modeling to inform management (Caudle et al. 2013). Each Ecological Site Description in the Ecological Site Information System (NRCS 2013) includes a wealth of useful information. Our toolkit has been informed and enhanced by the agencies’ work, but the two approaches differ in a few key ways. One difference is the degree to which plot-based data “drives” modeling. The agencies first create ecological site and state-and-transition concepts using existing records and expert knowledge and secondly collect field data in plots that are randomly and subjectively placed to test the concepts and describe and define the ecological sites and their states. In our alternative approach, stratifying study plots across gradients discussed in Step 1 requires conceptualization, but we emphasize the use of plot data as the primary foundation for defining and describing the ecological sites and their states. A second difference between the official and alternative approaches is the role of maps. The U.S. government has created soil maps for the majority of the country. Soil map polygons typically contain multiple soil types classified per U.S. soil taxonomy and *in situ* conditions (Soil Survey Staff 1999). Each soil type corresponds with one official ecological site. Because the soil types are undifferentiated on soil maps, multiple ecological sites can exist in one soil map unit (Soil Survey Staff 2013). Accordingly, ecological sites exist at spatial scales smaller than the scale of the basic map unit. A potential

problem is misinformed management planning founded on a false sense of the scale of the ecological site. Researchers are working towards mapping soils at higher resolutions to mitigate this problem (Duniway et al. 2010), but such maps are not yet widespread. In contrast with the governmental approach, we do not formally link our classification with maps. We believe this helps to mitigate possible confusion. A third difference between the official and alternative approach is the lexicon used to describe vegetation dynamics. Official state-and-transition models label temporal changes in grassland species assemblages “community pathways” within a grass state, even when the change is from exotic to native dominance or vice versa (NRCS 2013). The change from exotic to native dominance is a basic goal of California grassland restoration, and the “community pathway” nomenclature may underestimate the value that society places on a change from exotic to native dominance. In our approach, such nomenclature is not rigid. For instance, in the case study below, we refer to an inter-annual change in the grassland community as a transition between states. This sort of flexibility can help preserve the widespread utility of state-and-transition models (Jackson et al. 2002).

Step 3 - Identify causes of transitions or stalled recovery

In the toolkit framework, restoration can be considered a transition from an undesirable to a desirable state. The persistence of an undesirable state can indicate a recovery constraint: processes and/or factors that contribute to the resistance of degraded communities to restoration management. Knowledge about the temporal conditions that coincide with transitions, as well as the recovery constraints working against desired transitions, is invaluable for management prioritization and planning (Step 4).

Pairing the results from the state-and-transition modeling with data on temporally-dynamic environmental conditions can isolate the circumstances that are prerequisites for community succession on each ecological site. A classification tree (Breiman et al. 1984) can be used for this purpose. In the model, the dependent categorical variable represents the transition or lack of transition (hereafter “non-transition”) that occurred during a given transition year at a given plot. Independent variables represent the temporal conditions that occurred at each plot during the year the transition was detected (Jackson & Bartolome 2002). The classification tree will indicate the relative importance of the independent variables (conditions) to the variability of the categorical dependent variable (transitions/non-transitions). Conditions higher on the classification tree have stronger control over temporal dynamics of the ecological site than those lower on the tree, with the top, “root,” node having the greatest influence (De'ath & Fabricius 2000; Zuur et al. 2007). Relationships between the transitions and conditions will necessarily be constrained to the spatial and temporal scales of the data collection, but we hypothesize that the relationships can be predictive, as well.

Management teams faced with long-term persistence of unwanted states may require additional information on recovery constraints, which may not be isolated by the classification tree analysis. Recovery constraints can range from local-scale interactions such as trophic interactions and exotic species impacts on soil properties and nutrient cycling to long-term, regional-scale processes such as changes in disturbance regimes and availability of seeds due to landscape connectivity. Management intervention may be necessary to overcome recovery constraints that are forcing states to persist. Expanding understanding beyond plot-based observations of temporal conditions, to the mechanisms underlying the persistence of an undesirable state, can be achieved through small-scale sampling or manipulative

experiments. For example, a land manager hoping to foster a transition from high exotic cover to high native forb cover can assess the potential for natural recruitment of native species with seed bank soil samples. In another instance, if a land manager is concerned about the potential recolonization of exotic species in a restored area, the land manager can assess potential seed inputs by clearing a few small areas, ideally in a gradient from a nearby uncleared site, and observe which species establish.

Step 4 - Predict and prioritize the objectives, timing, sites, and treatments that will help achieve conservation goals

As stated above, we assume the management team will set general, idealistic conservation and restoration goals before undertaking the steps of the toolkit. An example of a goal is “enhance native forb abundance”. A complementary objective would specify how that goal could be achieved, for instance, “decrease exotic annual grass biomass by 50% during March, April, and May, to promote ample sunlight and moisture for native forbs” (Bush 2006). Results from the modeling in Step 3 can help the management team determine specific objectives and predict which timing, sites, and treatments have the highest potential for accomplishing the objectives. The team can plan its management activities using those predictions.

In non-equilibrium valley grasslands, it can be expected that management actions will be constrained by the timing and amount of rainfall. Managers must be prepared to implement treatments opportunistically, during the unique windows of time when conditions are auspicious for meeting restoration targets (Westoby et al. 1989; Holmgren & Scheffer 2001). Identifying the temporal conditions that co-occur with desired transitions (Step 3) can inform sets of plans to be deployed when proper conditions arise.

In addition to temporal constraints, managers of Californian grassland also typically have extensive land, but limited financial resources (Huntsinger et al. 2007), and therefore must prioritize sites and restoration treatments (Hopkinson et al. 2009; Meinke et al. 2009; Noss et al. 2009). Predicting the sites with the highest potential for successful treatments can guide site prioritization during the planning process. For instance, in valley grasslands, it may be hypothesized that on a particular ecological site, low levels of RDM left on the ground at the end of the dry season may be prerequisite to a desired transition detected during the subsequent rainy season. The management team could elect to use prescriptive livestock grazing or mowing to achieve low levels of RDM in order to create conditions that are auspicious for the desired transition. On a different ecological site, rodent bioturbation could be the prevalent temporally dynamic condition coinciding with the stability of a single, unwanted state. A possible management action for this ecological site would be eradicating the rodents, which would likely be very difficult as well as controversial among stakeholders. The management team may decide that the rodent recovery constraint is not worth mitigating and instead turn their attention to the ecological site without the rodent problem.

Another example illustrates how the models from Step 3 can inform predictions about, and prioritization of, treatments at a particular ecological site. If classification tree modeling reveals that light but increasing precipitation in October, November, and December predicates a desirable transition on a given ecological site, the management team will be faced with a conundrum. The Mediterranean climate requires that seeds of desirable species be planted in October, when light and soil temperature conditions are most favorable. Unfortunately, even if the rain in October is matching the weather signature isolated as ideal by the classification

tree, the team will not know with certainty that November and December will follow suit. Faced with this uncertainty, the team may elect to focus its efforts on treatments other than seeding at the ecological site.

Assessment of recovery constraints on an ecological site may also influence its prioritization. A site with a single constraint may require less effort and be prioritized over a site with multiple constraints (Suding et al. 2004). To ensure achieving the desired transition of a site with multiple constraints, the management team should attempt to tackle those constraints in one effort. The management team can use augmentative restoration, a restoration strategy that is synergistic with tackling multiple constraints, to guide the development and subsequent execution of any management plans. Augmentative restoration aims to enhance ecological processes that are necessary for the recovery of target plant communities but are not operating at adequate levels (i.e. recovery constraints). Under this approach practitioners have developed a suite of potential factors that can be modified to improve plant establishment (Bard et al. 2004).

Along with predicting and prioritizing temporal windows, sites, and treatments that will foster the achievement of goals and objectives, the science-based management team should also consult restoration literature and other managers for best practices. Using site-specific data to inform management decisions is an intuitive process that is gaining a new foothold with web-based databases. For instance, the Nature Reserve of Orange County (<http://www.naturereserveoc.org/>), which coordinates the land management activities of governmental and private landowners in a southern California land reserve system, has built a web-based database through which landowners can access useful ecological data, learn what other landowners are doing, and share information about their own management.

Step 5 - Opportunistic and adaptive management

Adaptive management is the process through which management is initiated, evaluated, and refined (Holling 1978). It differs from traditional management approaches by recognizing and preparing for the uncertainty that inevitably complicates resource management decisions. A typical formal adaptive management process consists of a multi-step cycle (Nyberg 1999; Murray & Marmoneck 2003; Reever-Morghen et al. 2006). The cycle promoted by the Forest Service of British Columbia, Canada consists of six steps (Table 1; Nyberg 1999; Murray & Marmoneck 2003). The first step, assessing the problem, includes setting goals and objectives, identifying possible actions that could be taken to achieve the goals, and identifying key uncertainties about the managed system. The second step is designing a plan that will foster the achievement of goals and test hypotheses about the system; the third step is implementing the plan. Next, in the fourth step, the management team monitors the implementation and effectiveness of the plan with attention to the key uncertainties identified in the first step. In the fifth step of the adaptive management cycle, the team evaluates the plan's outcomes. If the evaluation reveals that the desired outcome was not reached, managers move on to the sixth step and adjust their hypotheses and plan by returning back to the beginning of the six-step cycle. Table 1 contextualizes our toolkit with this six-step adaptive management cycle.

Table 1. A comparison of the toolkit with a 6-step adaptive management cycle

Adaptive management	Toolkit for science-based restoration of California grasslands
1. Assess problem	1. Describe species composition and its probable controls at study plots 2. Organize plot data into ecological site and state-and-transition models 3. Identify causes of transitions or stalled recovery
2. Design a plan	4. Predict and prioritize the objectives, timing, sites, and treatments that will help achieve conservation goals
3. Implement the plan	5. Opportunistic and adaptive management
4. Monitor plan implementation and effectiveness	5. Opportunistic and adaptive management
5. Evaluate the results	5. Opportunistic and adaptive management
6. Adjust plans and practices based on what was learned. Return to 1. Assess problem	Return to 3. Identify causes of transitions or stalled recovery; or 1. Describe species composition and its probable controls at study plots

Six-step adaptive management cycle per Nyberg 1999; Murray & Marmoneck 2003.

We do not discuss monitoring or evaluation in detail here, so we refer the reader to the Landscape Toolbox at <http://www.landscapetoolbox.org/>. This website is a valuable repository for field and remote sensing monitoring methods designed to inform managers' method selection, with attention to appropriate scale (Karl et al. 2011). The conceptual foundation of the Landscape Toolbox is consistent with the integrated framework for science-based management of arid lands put forth by Herrick and others (2006), discussed above. Herrick et al. (2012) expand this work by integrating ecological site-based monitoring and assessment into an adaptive management strategy for rangelands.

Like teams managing rangelands worldwide, teams managing California grasslands can benefit from the tools offered in the Landscape Toolbox as well as the restoration toolkit we propose here. We believe that our toolkit allows for substantial improvement in effectively achieving conservation goals as we show in Case Study 2.

CASE STUDY 2: USE OF THE TOOLKIT IN SOUTHERN CALIFORNIA VALLEY GRASSLAND

Here we illustrate the use of the toolkit in the valley grasslands of the Tejon Ranch, California (Figure 1). We elected to use Tejon Ranch as an example in favor of the East Bay Regional Park District (Case Study 1) for two main reasons. Primarily, valley grasslands in the southern part of the state have been underrepresented in the scientific literature in comparison with their more northerly counterparts. Secondly, Tejon Ranch is an ideal laboratory for our toolkit due to the exceptional areal extent of its grasslands (i.e. 48,000 ha),

the variation in its topography and soils, and the high abundance of natives compared with grasslands statewide (Hopkinson et al. 2009).

The mission of the Tejon Ranch Conservancy (hereafter, Conservancy) is to preserve, enhance and restore native species biodiversity on Tejon Ranch. The Conservancy is using the toolkit in a framework of adaptive, opportunistic management (Tejon Ranch Conservancy 2013). Cattle grazing is the Conservancy's primary on-the-ground management tool. Livestock have grazed the ranch since at least its founding in 1843, and the current cattle grazing regime consists of light to moderate stocking rates with minimal rotation between large, heterogeneous pastures (see Case Study 1 for additional information about the study area).

Step 1 - Describe Species Composition and its Probable Controls at Study Plots

The Conservancy is using the toolkit approach to manage grasslands across the entire ranch, but we constrain our example to the grasslands on the ranch's northern side. The southern side will need to be modeled separately because the Tehachapi Mountains bifurcate the ranch, and the grasslands south of the mountains are in a different regional climate zone than the grasslands north of the mountains (Bailey 1995). In total, 57 permanent plots have been established across 48,000 ha of grasslands ranch-wide, but the data populating the models in this case study are from only 30 plots established across 22,000 ha of Valley Grassland on the ranch's north side.

Study plots were randomly sited to ensure unbiased sampling. To capture the variation in soils and grassland "nativeness," the plots were stratified by the major geophysical areas on the north side of the ranch: San Joaquin Valley, Sierra Nevada, Tejon Hills, and Tehachapi Mountains. Sampling was conducted during the spring peak growing season in 2010, 2011, and 2012.

Each 3024 m² elliptical plot comprises four 25 m transects radiating in the cardinal directions from the corners of a 100 m² relevé. We sampled topographic factors at the spatial scale of the entire plot, soils at the corners of the relevé, and species on the transects. We assume relationships observed between the environment and species observed at the 3 × 10³ m² plots scale up to the extent of the landscape units of 10⁴-10⁵ m² (Bestelmeyer et al. 2011a) that aggregate into ecological sites. Here we describe the sampling of probable controls on species composition; sampling of the species composition itself is described in Case Study 1.

As this was the first effort to describe environmental and species composition patterns on the ranch's grasslands, we sampled numerous environmental variables (34 in total). Future sampling efforts can be streamlined to include only the variables deemed essential by this first effort. The environmental data fall into two major subsets. The first subset contains variables measured once at each plot and treated as "constant/spatial" factors for the ecological site classification (Step 2). Topographic variables in this subset are slope, aspect, and elevation. Edaphic variables are phytolith content, depth to restrictive layer, bulk density, and select properties of soil samples augered from depths of 0-15 cm and 30-45 cm [percent sand, silt, and clay; pH; C_{total}:N_{total}; plant-available sulfate (SO₄-S); plant-available phosphate (PO₄-P); and exchangeable cations Ca²⁺, K⁺, Mg²⁺, and Na⁺]. Geology underlying each plot was obtained from maps by the late geologist David Dibblee. Data is also collected for a second, "temporal" subset, to be used to isolate conditions associated with transitions/non-transitions (Step 3). Field-based variables include cover of bare ground, litter, gravel, cobbles, and boulders at time of sampling and estimated use by cattle, rodents, wild pigs, and humans

since the first germinating rains of the growing season. This subset also includes monthly weather for each plot obtained from the PRISM climate model (PRISM Climate Group 2013). Seven of the 34 environmental variables, including geology, were useful for system description and understanding, but not for quantitative analyses. We excluded those seven descriptive variables as well as ten variables that were highly correlated with others, leaving seventeen remaining for quantitative analyses (bottom row of Table 2).

Table 2. Correlations between topo-edaphic properties and 2010 species composition

Set of topo-edaphic variables	Correlation
Slope	0.2590
Elev Slope	0.3816
Elev Heat Slope	0.4463
C:N Elev Heat Slope	0.4100
C:N Elev Heat Slope Depth	0.1740
<i>Ca²⁺ C:N Elev Heat Slope Depth</i>	<i>0.5474</i>
B.D. Ca ²⁺ C:N Elev Heat Slope Depth	0.5437
B.D. Ca ²⁺ C:N Elev Heat pH Slope Depth	0.5455
B.D. C:N Elev K ⁺ pH PO ₄ Sand Slope Depth	0.5461
B.D. C:N Elev Heat K ⁺ pH PO ₄ Sand Slope Depth	0.5432
B.D. Ca ²⁺ C:N Elev Heat K ⁺ pH PO₄ Sand Slope Depth	0.5427
B.D. Ca ²⁺ C:N Elev Heat K ⁺ pH PO ₄ PO₄ Sand Slope Depth	0.5341
B.D. Ca ²⁺ C:N Elev Heat K ⁺ pH PO ₄ PO₄ Sand Slope SO ₄ Depth	0.5294
B.D. Ca ²⁺ C:N C:N Elev Heat K ⁺ pH PO ₄ PO₄ Sand Slope SO ₄ Depth	0.4991
B.D. Ca ²⁺ C:N C:N Elev Heat K ⁺ Na ⁺ pH PO ₄ PO₄ Sand Slope SO ₄ Depth	0.4644
B.D. Ca ²⁺ C:N C:N Elev Heat K ⁺ Mg ²⁺ Na ⁺ pH PO ₄ PO₄ Sand Slope SO ₄ Depth	0.4356
<i>B.D. Ca²⁺ C:N C:N Elev Heat K⁺ Mg²⁺ Na⁺ pH PO₄ PO₄ Sand Slope SO₄ SO₄ Depth</i>	<i>0.4015</i>

The full set of topo-edaphic variables correlated with the species data at 0.4015, and the optimal subset correlated at 0.5474 per the BIO-ENV routine (Clarke & Ainsworth 1993). Soil properties in bold were from soils sampled at 30-45 cm depth; all other soil properties were from 0-15 cm depth samples. “B.D.” denotes bulk density; “Depth” denotes depth to restrictive soil layer; “Heat” represents heat load, a proxy for aspect; and “Sand” denotes percentage of sand in the soil. Additional details about the variables can be found in the text.

Given the hypothetical placement of Tejon Ranch’s grasslands on the non-equilibrium end of the theoretical continuum, as well as the general support for the idea that topo-edaphic factors control species composition, we hypothesized that our topo-edaphic metrics would “explain” plant community structure. We verified this hypothesis using a BIO-ENV modeling approach (Table 2; Spearman correlation, Sørensen dissimilarity for the community data matrix, Euclidean distance for the log-transformed topo-edaphic data matrix, 53 species after omission of species encountered in only a single plot). We found that the full suite of topo-edaphic variables ($n = 17$) was correlated with the species composition data at 0.4015. We perceived this correlation as sound rationale to proceed with classifying landscape units based on their topo-edaphic properties. The subset ($n = 6$) with the highest correlation, 0.5474, contained soil exchangeable Ca²⁺ (0-15 cm depth sample), soil C:N (0-15 cm depth sample), elevation, heat load (a proxy for aspect; McCune and Keon 2002), slope, and soil depth. Subsequent sampling efforts can be streamlined using this subset as a guide.

Step 2 - Organize Plot Data into Ecological Site and State-and-Transition Models

The “constant/spatial” topo-edaphic data collected at the 30 study plots resolved into five ecological sites per hierarchical cluster analysis (Figure 4; Euclidean distance measure, Ward’s linkage, 17 continuous log-transformed variables). A Mantel test run on the cluster dendrogram (Borcard et al. 2011) identified five as the optimal number of clusters ($r = 0.49$). Conditional box plots with the five clusters as the categorical independent variable and 17 continuous environmental variables as the conditional variables revealed the key variables driving the differences between ecological sites (Verfaillie et al. 2009). We used a non-parametric Kruskal-Wallis analysis of variance to test for differences between groups (Whitlock & Schluter 2009) with respect to the key variables. We included geologic characteristics in ecological site names for ease of communication among stakeholders, even though geologic variables were not in the quantitative cluster analysis.

The ‘Flat sands and loamy sands on Holocene surficial sediments’ ecological site comprises sites that lie at low elevations of the ranch (~150-450 m). Its surface soils (i.e. soils sampled at 0-15 cm and 30-45 cm) have low $\text{SO}_4\text{-S}$ compared with the surface soils of the other ecological sites. Generally situated at elevations slightly higher than the previously described ecological site, the ‘Gently sloping sandy loams on dissected alluvial terraces’ ecological site has lower surface soil C:N than the other ecological sites. Sites composing the ‘Sandy clay loams on steeply-sloped, low-relief hills of Miocene sediments’ ecological site lie on marine and nonmarine sediments deposited during the Miocene when the Great Central Valley was an inland sea. In comparison with the surface soils of the other ecological sites, surface soils of this ecological site have low $\text{PO}_4\text{-P}$, high $\text{SO}_4\text{-S}$, and high exchangeable Ca^{2+} and Na^+ . The ‘Moderate slopes on Pleistocene landslide debris’ and ‘Steep slopes on Sierran plutonic basement complex’ ecological sites lie on mountainous terrain at a wide range of elevations.

For the remainder of the case study, we use the ‘Flat sands and loamy sands on Holocene surficial sediments’ ecological site, (hereafter “Flat sands ecological site”) to illuminate our approach. The Conservancy has prioritized this ecological site for management because of its demonstrated potential to support desired native plant communities as well as special status wildlife species (Tejon Ranch Conservancy 2013). Several objectives aimed at maintaining and enhancing the ecological site’s native vegetation are synergistic with objectives for its wildlife, but here we focus only on the vegetation.

We offer an ecological site classification, not an ecological site map; however, we used existing maps of local geology, soils, and elevation; visual cues of slope; and informal texture-by feel estimates to approximate the areal extent of the Flat sands ecological site. We estimate it covers approximately 3600 ha ($3.6 \times 10^7 \text{ m}^2$), not necessarily contiguously, on the western edges of the ranch north of the Tehachapi Mountains.

Within those estimated 3600 ha, eight U.S. soil map units (soil map polygons) occur once or repeatedly. The eight map units comprise 17 undifferentiated soil types, two of which correlate with official ecological sites. Within the estimated area, the Arvin soil correlates with ‘R017XF072CA Dry Coarse Loamy’ and the Steuber soil correlates with ‘R018XE032CA Coarse Loamy Fan’ and ‘R018XE006CA Fine Loamy’ (Soil

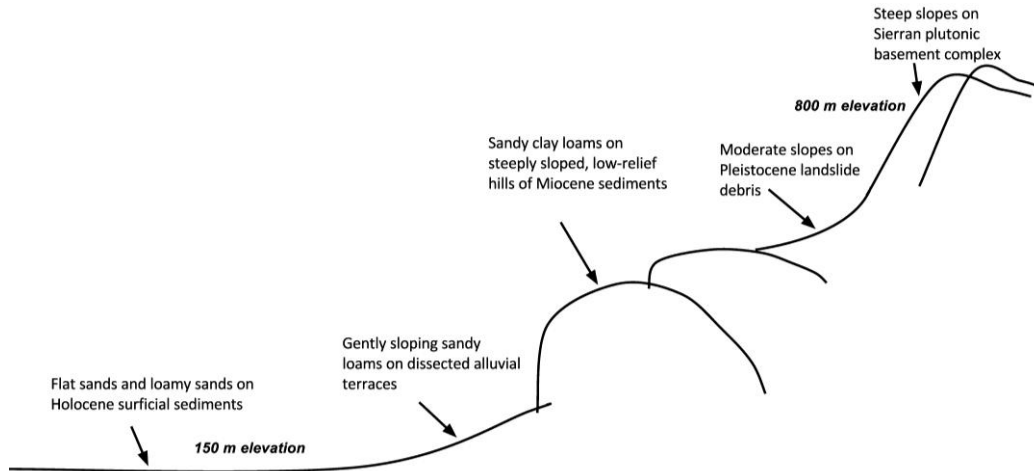


Figure 4. Ecological sites on a schematic cross-section of the characteristic landforms underlying the grasslands on the northern half of Tejon Ranch. The ecological sites were classified using topo-edaphic data collected at 30 randomly located study plots across 22,000 ha of valley grasslands. We assume data collected at the plots ($3.6 \times 10^3 \text{ m}^2$) scales up to landscape units of $10^4 - 10^5 \text{ m}^2$, and we estimate that the landscape units aggregate into ecological sites that cover $\geq 10^7 \text{ m}^2$. The ecological sites are arrayed in a mosaic across the landscape, but are depicted here along a simple elevational gradient to illustrate general associations among topography, geology, and ecological sites.

Survey Staff 2013). Future work could include intensively relating our Flat sands ecological site with these three officially-described ecological sites. As of the writing of this chapter, Ecological Site Descriptions for the three ecological sites were not published in the Ecological Site Information System (NRCS 2013).

To identify states and transitions (Figure 5), we ran hierarchical cluster analysis (Sørensen dissimilarity; flexible beta linkage set at -0.25) on 21 plot \times years (7 plots in the ecological site \times 3 years of vegetation sampling). The dataset comprised thirty-five species (species encountered in more than one plot \times year, square-root-transformed relative cover). We objectively cut the dendrogram to nine clusters using a randomization procedure with Indicator Species Analysis (Dufrene & Legendre 1997; McCune & Grace 2002). Next we modified the nine species composition clusters *a posteriori* based on Conservancy goals and on-the-ground knowledge not identified by the model. Because the enhancement of native forb communities is among Conservancy objectives, clusters that had functional overlap in species composition were combined into states (two clusters were lumped into the ‘Native annual forbs characteristically abundant state’; five clusters were lumped into the ‘Exotic annual grass dominant’ state). In addition, the composition at two plot \times years was very distinct (i.e. low cover of live vegetation paired with either high litter cover or high litter and bare ground cover), but because we input relative cover, the cluster model was not sensitive enough to pick up this distinction. We removed those two plot \times years from their clusters, and designated each as a state (‘Sparse live vegetation, litter dominant’; ‘Sparse live vegetation, litter and bare dominant’). ‘Dominance’ and ‘characteristic abundance’ in state names were defined with respect to mean relative cover across all plot \times years in the state (species or functional groups with $\geq 40\%$ mean relative cover were classified as dominant; those with $>40\%$ mean relative cover were classified as “characteristically abundant”).

The resulting state-and-transition model for the Flat sands ecological site (Figure 5) consists of six states (boxes), five transitions (straight arrows), and two non-transitions (curved arrows). The catalogue of states adjacent to the boxes and arrows describes species composition of each state. The catalogue of transitions lists hypotheses about why the transitions and non-transitions occurred and can be used to predict future dynamics. Transitions and non-transitions symbolized with solid arrows were linked to temporally-dynamic environmental conditions by a classification tree (Step 3; Figure 6); those with dashed arrows were linked to temporally-dynamic conditions by local knowledge. While the transitions and non-transitions occurred from 2010 to 2011, 2011 to 2012, or 2010 to 2012, we hypothesize that these are predictive with respect to inter-annual through decadal time scales.

Step 3 - Identify Causes of Transitions or Stalled Recovery

We used a classification tree to identify the temporal conditions co-occurring with state transitions and stability at the Flat sands ecological site during 2010-2012 (Figure 6). The dependent, categorical variable represented the seven transitions and non-transitions symbolized by the arrows in Figure 5. The independent variables were temporally-dynamic conditions that we hypothesize to be influences on vegetation succession: September-March monthly rainfall totals, litter cover, categorical cattle grazing severity, and rodent bioturbation.

In the data matrix, row headings were “plot \times transition years,” with transition year being the year the transition was detected. Each plot \times transition year was assigned a category representing the transition or non-transition detected at the plot during the year specified (Y variable) along with a unique set of temporal conditions that preceded or were concurrent with the detection of the transition or non-transition (X variables). Monthly rainfall totals are specific to each plot due to our use of the PRISM model (PRISM Climate Group 2013). The resulting data matrix had 14 rows (7 plots \times 2 possible transition years 2011 and 2012), one Y-variable “transition” column, and several X-variable “temporal condition” columns.

The classification tree isolated influences on four of the seven transitions/non-transitions that occurred (solid arrows in Figure 5; terminal node circles in Figure 6). The root node of the classification tree, representing the condition with the strongest overall effect, was December precipitation during the growing season in which the transition/non-transition was detected. Rainfall, an abiotic factor, had more control over community temporal dynamics than did the biotic interactions of litter cover, cattle grazing, and rodent bioturbation. This finding lends strength to the hypothesis that Tejon Ranch’s grasslands should be placed on the non-equilibrium end of the theoretical continuum from equilibrium to non-equilibrium.

Local knowledge about conditions on the ground was used to hypothesize causes of the remaining three transitions not identified by the classification tree (dashed arrows in Figure 5). Data-driven and local knowledge are recorded in the catalogue of transitions adjacent to Figure 5.

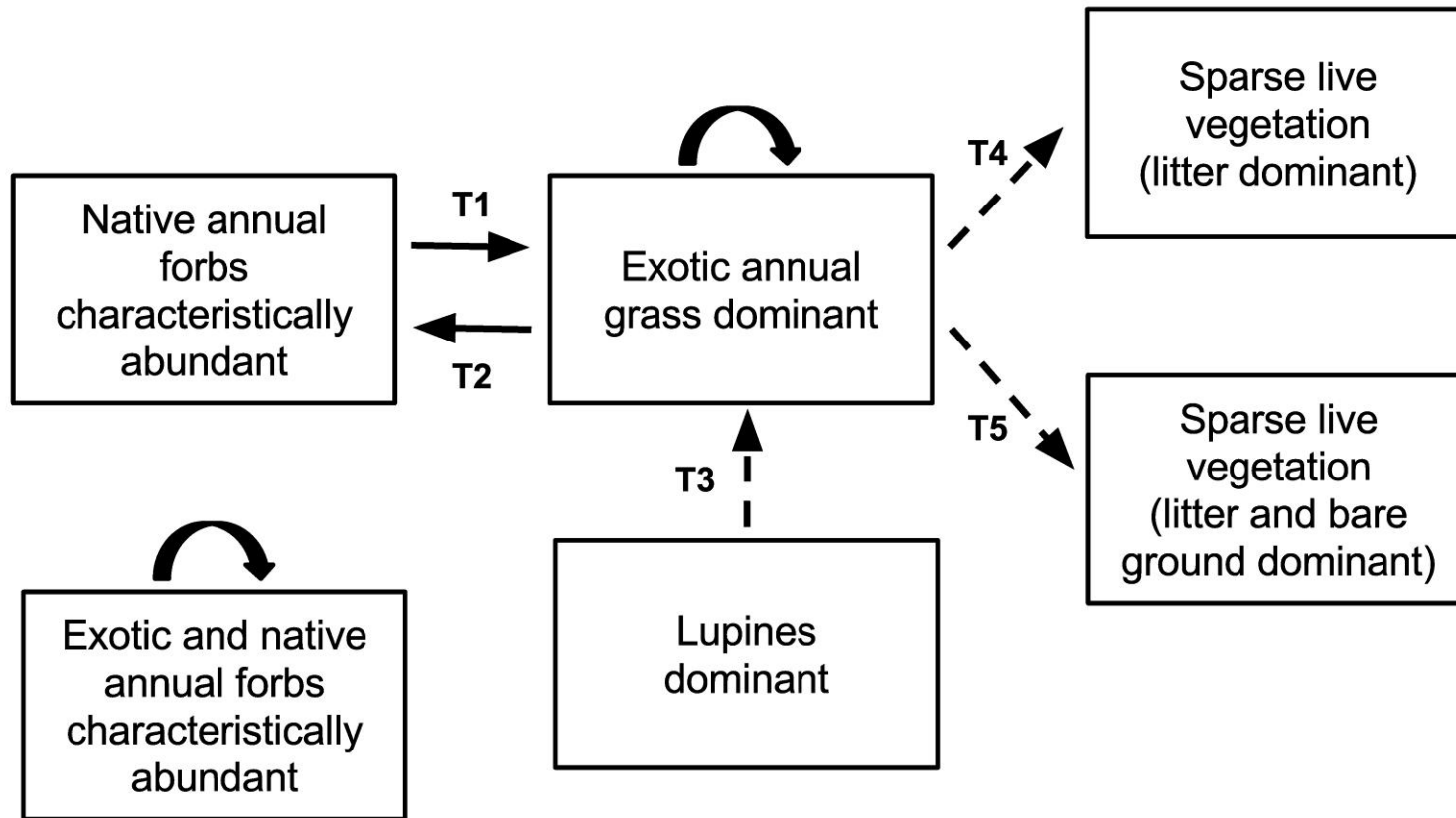


Figure 5. State-and-transition model for the ‘Flat, low elevation, sands and loamy sands on Holocene surficial sediments’ ecological site of Tejon Ranch. Transitions (straight arrows) and non-transitions (curved arrows) occurred during 2010-2012, but we hypothesize that they are predictive on inter-annual as well as decadal time scales. Transitions/non-transitions symbolized with solid arrows were linked to temporally-dynamic environmental conditions by the classification tree in Figure 6; those with dashed arrows were linked to such conditions by local knowledge (see Catalogue of transitions).

Catalogue of states:

- Native annual forbs characteristically abundant (*Plagiobothrys* spp., *Trifolium* spp.)
- Exotic annual grass dominant (*Avena barbata*, *Bromus diandrus*, or *Vulpia myuros*)
- Lupines dominant (native *Lupinus* spp.)
- Sparse live vegetation, litter dominant
- Sparse live vegetation, litter and bare dominant
- Native and exotic annual forbs characteristically abundant (*Dicholostemma capitatum* (native) and *Erodium botrys* (exotic). Native forb cover is, on average, less than that of 'Native annual forbs characteristically abundant'.)

Catalogue of transitions:

(Temporal conditions and transition/non-transition occurred during the same September-May growing season.)

Transition 1 (T1): Native annual forbs characteristically abundant → Exotic annual grass dominant

This is an undesirable transition in relation to Conservancy goals.

Temporal conditions (classification tree): December rainfall greater than or equal to 120 mm.

Transition 2 (T2): Exotic annual grass dominant → Native annual forbs characteristically abundant

This is a desirable transition in relation to Conservancy goals.

Temporal conditions (classification tree): December rainfall less than 120 mm and litter covering less than 5% of the ground.

Transition 3 (T3): Lupines dominant → Exotic annual grass dominant

This is an undesirable transition in relation to Conservancy goals.

Temporal conditions (local knowledge): This transition was likely linked to high December rainfall.

Transition 4 (T4): Exotic annual grass dominant → Sparse live vegetation (litter dominant)

Neutral in relation to Conservancy goals, but succession should be monitored

Temporal conditions (local knowledge): This transition occurred between 2011 and 2012. It was likely linked to the heavy production of grass in the 2010-2011 growing season and the lack of fire and livestock grazing in 2011-2012.

Transition 5 (T5): Exotic annual grass dominant → Sparse live vegetation (litter and bare ground dominant)

Neutral in relation to Conservancy goals, but succession should be monitored

Temporal conditions (local knowledge): This transition was likely linked to a fire that burned through part of the Ecological Site in September 2011.

Non-transition: 'Exotic annual grass dominant' persisted

Undesirable in relation to Conservancy goals

Temporal conditions (classification tree): December precipitation below 120 mm, litter covering greater than 5% of the ground, and September precipitation exceeding 2 mm. If this state persists for the long-term, recovery constraints should be investigated using manipulative experiments.

Non-transition: 'Exotic and native annual forbs characteristically abundant' persisted

Neutral in relation to Conservancy goals, but succession should be monitored

Temporal conditions (classification tree): December precipitation below 120 mm, litter covering greater than 5% of the ground, and September precipitation below 2mm.

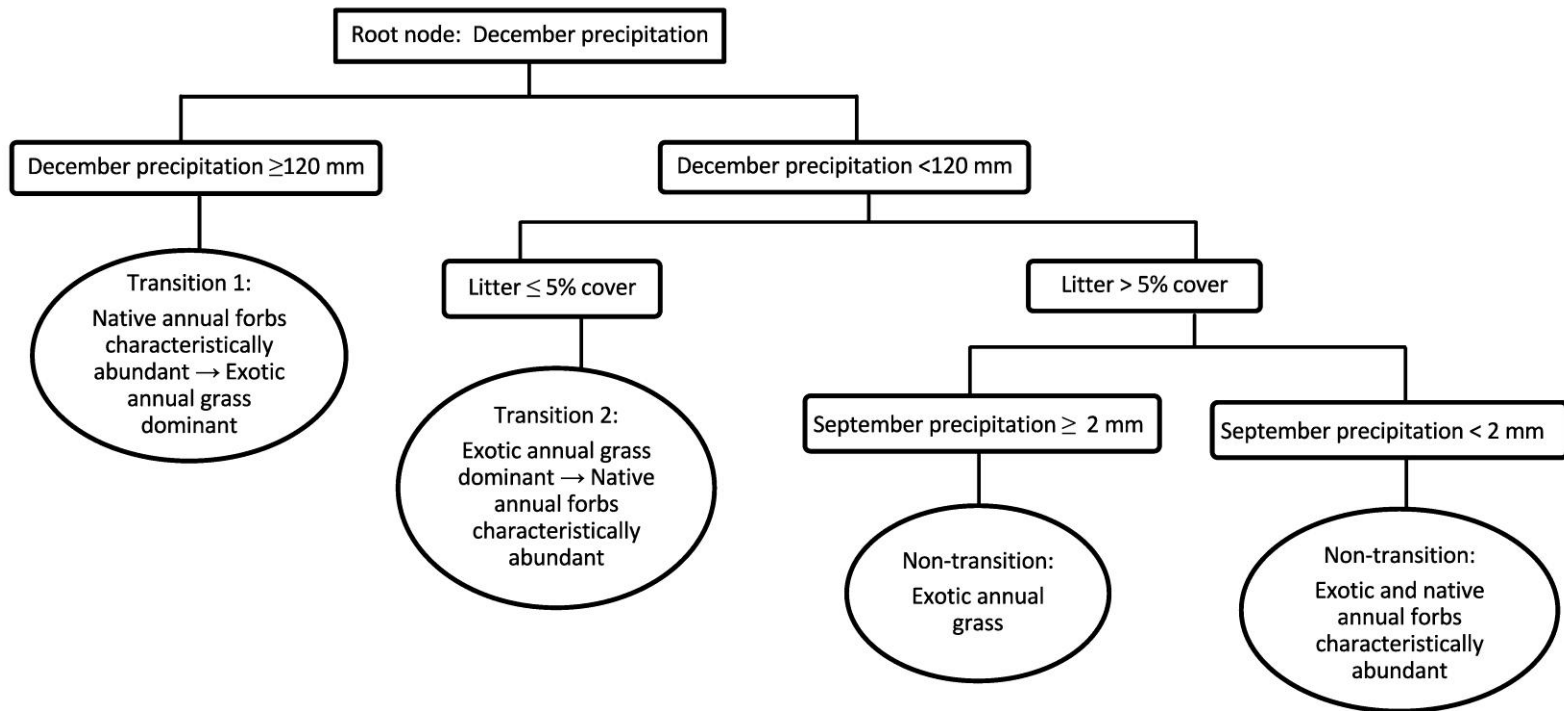


Figure 6. Classification tree identifying temporal environmental conditions predicating transitions/non-transitions at the Flat sands ecological site. The tree identified conditions for four of the seven transitions/non-transitions observed in 2010-2012. Terminal nodes (circles) represent the transitions/non-transitions that the tree linked to conditions; conditions are in the squares preceding the terminal nodes. For example, rainfall greater than or equal to 120 mm in December was the prerequisite of T1: 'Native annual forbs characteristically abundant → Exotic annual grass dominant'. The December rainfall and detection of T1 occurred during the same September-May growing season. Conditions higher on the classification tree have stronger control over community dynamics on the Flat sands ecological site than those lower on the tree.

Step 4 - Predict and Prioritize the Objectives, Timing, Sites, and Treatments That Will Help Achieve Conservation Goals

In light of its management goal to "Preserve, enhance and restore native biodiversity," the Conservancy may prioritize objectives, timing, and treatments that facilitate T2: Exotic annual grass dominant → Native annual forbs characteristically abundant (Figures 5 and 6). The classification tree analysis in Step 3 specified that the prerequisite to this transition is plant litter at <5% ground cover in the spring following a December with low rainfall (< 120 mm). Accordingly, the Conservancy would specify an objective such as "maintain <5% ground cover in the spring following a December with low rainfall to facilitate T2". The team would elect cattle grazing as the treatment type because it is the most powerful on-the-ground treatment option. To achieve its objective, the Conservancy must opportunistically capitalize on low December rainfall and may be challenged to find a livestock operator who can manage with this degree of flexibility. An alternative tactic that would not require such flexibility would be consistently maintaining springtime litter ground cover levels at 5% or less on the areas of the ecological site with the 'Exotic annual grass dominant' state, thereby creating conditions auspicious for the desired transition if a dry December does occur.

The classification tree indicates that minimal springtime plant litter is prerequisite to T2, but it does not stipulate the role of litter in T1 (Native annual forbs characteristically abundant → Exotic annual grass dominant). The classification tree links T1 only to a wet December. Because the model indicates that T1 is beyond human control, the Conservancy may elect to turn its attention to different transitions, especially those that the classification tree links with manipulatable conditions.

Other management teams, however, may not have the luxury to turn their focus elsewhere. A hypothetical scenario involves a team that is managing the ecological site having a mandate to spend restoration funding by the financial year-end (i.e. the June following the wet December). A possible restoration strategy would be using livestock on the areas of the ecological site dominated by exotic annual grass to reduce grass growth, cover, and seed production while not reducing native annual forb populations (but see Kimball & Schiffman 2003). The management team would work with the livestock operator to turn the cattle out during the wet December but remove them when desirable native species begin to set seed. Because the team would be adopting a strategy that is not explicitly prescribed by the data, we would recommend incorporating timely effectiveness monitoring.

Step 5 - Opportunistic and Adaptive Management

Upon completion of the treatment (using cattle to maintain springtime litter at <5% ground cover during a growing season with December rainfall < 120 mm) to foster T2 (Exotic annual grass dominant → Native annual forbs characteristically abundant), the Conservancy would monitor and evaluate the results of the treatment. If the desired litter levels were achieved within the specified weather signature, but the desired transition did not occur, the Conservancy would adapt its hypotheses about the causes of T2 by returning to toolkit Step 3. If a repeated return to Step 3 does not result in the achievement of restoration goals, the Conservancy may elect to return to Step 1 to re-assess the probable controls on species composition of the grasslands of Tejon Ranch.

CONCLUSION

California's grassland restoration managers bear the important responsibility of preserving and restoring native plant communities. They face many challenges, including widespread exotic species, land use changes, and extreme spatial and temporal variability. We propose a set of conceptual tools to help them deal with these challenges.

Our proposed toolkit uses a general framework proposed by Begon et al. (1996) that the scientific knowledge base for ecosystems proceeds through description to understanding into prediction. For managers predictions are in the end ideally tied into control of the system to achieve management goals (Bartolome et al. 2009). Adaptive management has been lauded as an effective management approach, but the expenses of detailed monitoring and long-term assessment mean that it is rarely executed. Westoby et al. (1989) proposed the state-and-transition approach as a compromise allowing for selection and adoption of management controls without waiting for complete understanding and prediction of system responses. The ecological site concept is also helpful to structure information about spatial and temporal variations and accordingly enhance ecosystem understanding, prediction, and ultimately control.

Rigorous adherence to the toolkit will not be appropriate for all management teams at all times, and teams can take a less structured approach by continually fine-tuning plans as monitoring reveals useful information and/or conditions change. For instance, a management team with a limited science budget may elect to sample a small set of environmental variables to develop an ecological site classification and fine-tune the model as money is available by sampling additional variables isolated through monitoring. If only a single year of species sampling can be conducted, the team could assign single-year vegetation states to the ecological sites. On the other hand, if monitoring reveals that extreme environmental changes (e.g., atmospheric nitrogen deposition, fire regimes) are impacting plant community structure, the management team may elect to shift its focus from the topo-edaphic and climatic controls on species composition emphasized by the toolkit to controls imposed by the extreme environmental changes.

We illustrated the use of the toolkit in the most extensive grassland type in California, Valley Grassland, but it is suitable for other spatially and temporally complex terrestrial ecosystems. This toolkit can help managers describe and understand the complexity and use their understanding to achieve their restoration goals.

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