



Rangeland vulnerability to state transition under global climate change

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Abstract

The rapid pace of global climate change necessitates tools for prioritizing limited climate-adaptation resources in the face of imperfect knowledge regarding plant community responses to changing climate. In addition, global climate change often leads to novel shifts in plant communities which are difficult to anticipate with detailed models based on current system dynamics, which are often greatly altered under novel climates. In order to identify nonforested plant communities that are highly susceptible to state transitions under global climate change, we examined differences between the historical climate envelopes and end-of-century projections. We developed a vulnerability index based on the realized climate envelope for a given plant community relative to future climate exposure under two different climate-forcing models. To provide an approach to prioritizing climate-change adaptation resources at smaller scales, we used scenario analysis to determine the probability of falling outside of the historical climate envelope for each vegetation type present in a given management unit. The large-scale index consistently identified several areas as highly vulnerable to ecosystem state transition under future global climate change. South and north central Texas, the northwestern Great Plains and Rocky Mountain regions, eastern Kansas, and large portions of central and western Texas appear most vulnerable under both climate models. Scenarios identified thresholds of potential state shift for every vegetation type in the small-scale management areas investigated. Our study identifies a simple method for determining the relative vulnerability of nonforested plant communities to state shifts, providing a robust approach for prioritizing limited climate-adaptation resources at multiple scales.

Keywords Rangelands · Scenario analysis · Alternative states

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1 Introduction

Given the importance of climate for controlling plant distributions, climate change is likely to lead to the reorganization of plant communities, with the likelihood that alternate community assemblages emerge increasing as the departure from historical climate conditions increases (Leemans and Eickhout 2004). This proposition is supported by paleoecological findings showing shifts in community composition since the last interglacial that have no analogue in earlier times and which closely track the occurrence of no-analogue climate conditions—unique combinations of temperature and precipitation in regions with distinct abiotic characteristics (Williams and Jackson 2007). Similar changes have been documented recently in areas with rapidly changing climatic characteristics resulting from contemporary climate change (Thuiller 2004). Models of future climate-change scenarios also predict a reorganization of communities beyond certain thresholds of change (Gonzalez et al. 2010; Grimm et al. 2013). Given a large enough magnitude of climatic change, plant community modification can be pushed past a tipping point resulting in a new state with different sets of reinforcing feedbacks (Higgins and Harte 2012). This often leads to the disruption of ecosystem function and a loss of the ecosystem services that were previously reliably provided (Mäler 2000). This has already occurred in a variety of ecosystems (Scheffer et al. 2001). In fact, climate change is identified as one of the most prevalent drivers of regime shifts in terrestrial ecosystems (Rocha et al. 2015). In addition, the more future environments differ from the present, the more incomplete our understanding of ecological interactions will be, opening the door for ecological surprises that interfere with our ability to accurately predict community responses to global climate change.

A vast amount of uncertainty surrounds attempts to estimate plant community trajectories in the face of climate change (Lawler 2009). Large error associated with projecting climate coupled with uncertain future trajectories of emissions and attendant changes in temperature and precipitation results in an array of potential futures regarding precipitation and temperature estimates for the upcoming decades (Randall et al. 2007). In addition, species-specific responses to changes in temperature, precipitation, and increases in atmospheric CO₂ and N make species-level responses difficult to predict (Walther et al. 2002). In considering community responses, one must also determine the potential changes in positive and negative species interactions under different combinations of climatic variables (Gilman et al. 2010). Given this uncertainty, accurate future predictions of species composition, or models of species assembly that can account for future uncertainty are a long way off, but managers are expected to develop climate-change adaptation plans despite the inadequacy of current science to anticipate its impacts.

A need to develop ecosystem management plans for climate-change mitigation and adaptation in the face of limited knowledge of potential system-specific responses and limited resources for implementing adaptation has driven a proliferation of climate-change vulnerability analyses (Füssel and Klein 2006; Preston et al. 2011; Watson et al. 2013). While some analyses, such as dynamic global vegetation models, incorporate complex interactions, and specific mechanistic drivers of vegetation response to climate change, the majority consist of general conceptual vulnerability frameworks meant to transcend specific cases or systems (Füssel 2007). Regardless of the level of complexity, most vulnerability frameworks recognize the importance of including measures of both exposure and sensitivity to altered climatic conditions to determining relative vulnerability of ecosystems to climate change (Füssel and Klein 2006). Exposure is a measure of the level of change in

important climate variables at a given locale, which differs as a result of spatial variability in the response of climate to increased atmospheric CO₂ (Füssel 2010; IPCC 2007). Sensitivity describes the degree to which an ecosystem is affected by changes in climate variables and their interaction (Füssel 2010; IPCC 2007). Predicting the relative magnitudes of system responses to changing climate requires an integration of these two components of vulnerability.

Vulnerability analyses useful for prioritizing rangeland ecosystems are largely absent from the recent proliferation of climate vulnerability analyses. Those aimed at determining relative vulnerability in forested systems are largely inappropriate for rangeland ecosystems because they often focus on climate envelopes for dominant tree species (Clark et al. 2011; Heikkinen et al. 2006) and rangelands are often comprised of a mix of species and functional groups. Management of nonforested systems is often focused on preventing state shifts toward less productive bare ground- or woody plant-dominated states (Bestelmeyer 2006; Briske et al. 2006), elevating the importance of understanding the potential for climate change to drive community alteration in these systems. In addition, rangelands dominate arid and semiarid environments, making them highly susceptible to changes in precipitation and increased evapotranspiration attendant to warming temperatures (Leemans and Eickhout 2004). Vulnerability analyses that are available for rangelands currently focus on exposure only, ignoring the importance of the dose-response relationship to changing climatic variables that is captured by integrating sensitivity into determinations of climate vulnerability (Briske et al. 2015; Joyce et al. 2013).

The objective of this study is to develop a set of vulnerability indices that integrates exposure and sensitivity of rangeland ecosystems to climate change in order to identify plant communities that are highly susceptible to ecosystem state transitions under global climate change. This study develops an approach to providing information at multiple scales for policy-makers and land managers to determine relative vulnerability of different rangeland plant communities to a range of possible of future climates in order to develop mitigation and adaptation strategies and prioritize funding and management needs accordingly. We assessed vulnerability to state shifts at two scales: (1) we developed a vulnerability index for the continental USA for use in prioritizing federal management investments; (2) we completed scenario analyses for four individual US Department of Defense installations to serve as examples of vulnerability assessments at the scale of management decision-making. Our approach can be adapted to incorporate new and emerging climate forecasting models as they are developed and can be used to identify areas where the development of more mechanistic models to determine potential plant community trajectories is most urgent.

2 Methods

2.1 Data

We used LANDFIRE existing vegetation-type landcover classifications to represent ecological states currently present at a given site. The existing vegetation-type data are derived from Nature Serve's Ecological Systems classification with additional units derived from National Vegetation Classification Standard alliances. These data are organized into ecological systems as functional units that represent biological communities that are influenced

by similar dynamic ecological processes such as fire or flooding. They are based on a Landfire field-referenced database which combines all available georeferenced data (e.g., Forest Service Forest Inventory and Analysis data) (Rollins 2009). Geospatial data on indicator species, topography, soils, gradients of environmental data, and disturbance regimes are used to further refine classification (Comer et al. 2003). In this regard, they are amenable to analyses aimed at understanding direct impacts of climate change on ecological communities and indirect impacts resulting from disturbance regime change. This is crucial as vegetation changes in nonforested ecosystems are often highly dependent upon altered fire and flooding regimes.

We determined a theoretical historical climate envelope for each nonforested vegetation state delineated by the LANDFIRE existing vegetation types by determining historical average annual precipitation and mean annual temperatures (30-year normal, 1981–2010; PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>) at 1-km resolution. LANDFIRE and climate data were downloaded at their original resolution (30 and 800 m, respectively) and resampled to 1 km using mode resampling for LANDFIRE and cubic resampling for climate data. The climate envelope for each vegetation state defined by LANDFIRE existing vegetation-type classifications was defined by the range of historical temperature and precipitation combinations present in the area delineated by a specific vegetation state (LANDFIRE existing vegetation type). We then calculated the future climate envelope for each LANDFIRE existing vegetation type by determining end-of-century projected average temperature and precipitation at a 1-km resolution and calculating the range of future temperature-precipitation combinations expected within each LANDFIRE existing vegetation type. The climate envelopes (historical and projected future) were therefore based on annual average temperature and annual accumulated precipitation for each cell of a given environment type. We used two different climate-forcing models (the HadleyCM3 model and the Parallel Climate Model (PCM)) to represent high and low climate sensitivities in terms of equilibrium of global mean surface air temperature to increasing CO₂ levels (IPCC 2007). We used the data for two emission scenarios: the A1 (high emissions continue) and the B1 (significant conservation and reduction of CO₂ emissions). The PCM B1 and HadleyCM3 A1 represent the extremes of possible outcomes from the climate analysis (Iverson et al. 2008). While we provide these two models as examples, our approach can be used with any existing climate-forcing model and can therefore be updated as new models are developed. Managers are likely considering management in the nearer term than the end-of-the century. However, we used end-of-century projections in developing our index because long-term climate-induced state shifts require more mitigation and adaptation planning and earlier action than shorter term weather fluctuations and attendant plant community dynamics. Therefore, our index is aimed at identifying areas that are vulnerable to state shifts, which are more difficult to adapt to and mitigate against than community compositional fluctuations. However, our approach can be used for projections at any temporal scale.

2.2 Relative vulnerability to state transitions among rangeland ecosystems of the continental USA

We calculated the Jaccard dissimilarity coefficient to determine the degree of overlap (Jaarsveld et al. 1998) between the historical climate envelope and end-of-century projections for each vegetation type. The Jaccard dissimilarity coefficient is calculated as follows:

$1 - [\text{the number of cells that remain within the historical climate envelope under the modeled projection} / (\text{the number of cells that fall outside the historical climate envelope under the modeled projection} + \text{the number of cells in the historical climate envelope that do not overlap with the projected climate envelope})]$. Each vegetation type will have an index value between 0 and 1 with higher numbers indicating greater probability of a vegetation-state shift as a result of that vegetation type experiencing climate severely departed from the historical climate envelope. An index score of 0 indicates complete overlap of historical climate envelopes and predicted climate for a given environment type while a score of 1 indicates no overlap. Thus, the index ranks each community from lowest vulnerability (index score = 0) to greatest vulnerability (index score = 1).

In addition, we explored the contributions of temperature and precipitation to differences in current and future climate envelopes for each nonforested vegetation type by plotting a probability density function to current and modeled temperature and precipitation data to explore overlap for each climate variable. The density function used a Gaussian kernel and Silverman's rule-of-thumb for determining the bandwidth for each vegetation type (Silverman 1986).

2.3 Site-specific ecosystem vulnerability to state transitions

In order to illustrate a method for prioritizing mitigation and adaptation over smaller scales, we examined the probability of falling outside the historical climate envelope for each vegetation type several military installation across the western USA. The Department of Defense owns and manages over 4 million ha in the USA (Vincent et al. 2017). While the purpose of these lands is to support training and mission-related activities, the Department of Defense is also tasked with managing its natural resources in order to maintain the ecological integrity of its training areas and the ecosystem services they provide (Vincent et al. 2017). Therefore, identifying appropriate management activities under future climate change is imperative for meeting Department of Defense objectives. In addition, management on Department of Defense land holdings is important to maintaining ecosystem services generally as they occur in a variety of ecosystems, have a variety of habitats and conditions as a result of training activities, and have relatively undisturbed large buffers around active training grounds (Tazik and Martin 2002). For these reasons, military installations have more species of plants and animals per unit area than the land holdings of all other US agencies and help support landscape-scale ecological processes and function in their regions (Stein et al. 2008). Given the uncertainty inherent in climate-forcing models, understanding the potential for climate-induced vegetation shifts under multiple scenarios could be more useful for managers of individual bases or other smaller land areas. The scenario most likely to occur at a given installation can be tracked as climate change progresses rather than assuming one or more climate models is accurate, allowing managers to prioritize the vegetation types on their managed lands according to the level of climate change actually occurring for that area.

We determined the probability of falling outside the historical climate envelope on Forts Hood, Bliss, Carson, and Riley, given scenarios of temperature increases between 1 and 10 °C. We chose these installations because they represent North-South and East-West gradients of climate conditions. However, this approach can be applied to any installation or land-management unit for which vegetation classification and historical climate data exist.

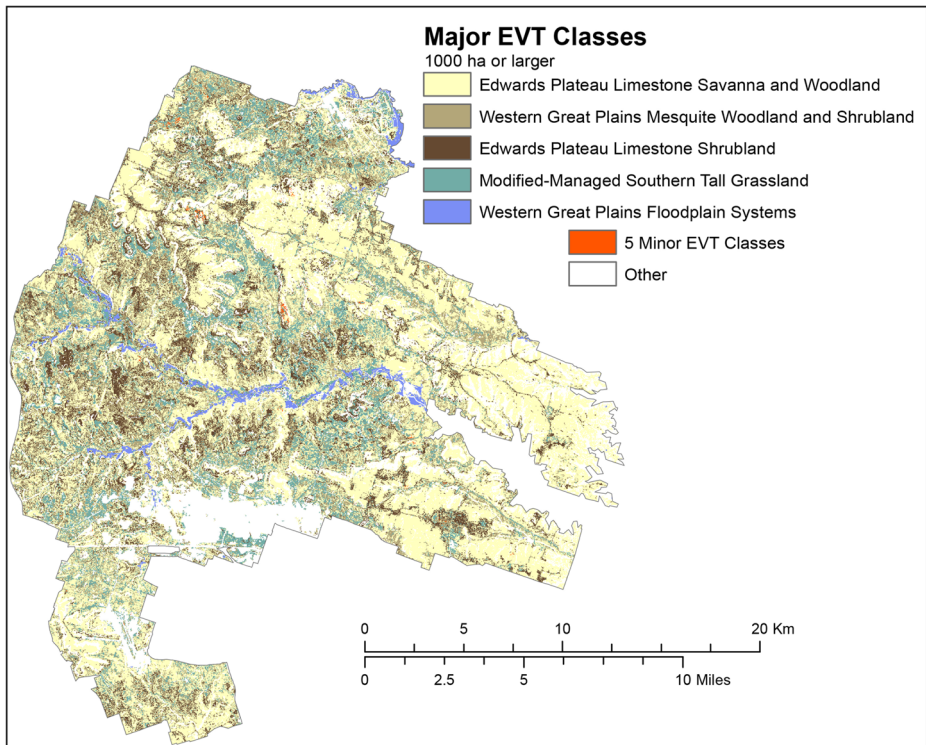


Fig. 1 Map of the major Landfire Existing Vegetation Types on Fort Hood. Only those comprised of more than 100ha are included. All others are included as “minor EVT classes.” Areas not classified by Landfire are labeled “other”

The Fort Hood installation includes 87,890 ha in the central Texas cross timbers and prairie vegetation region. Average annual precipitation is 81 cm with an average winter low of 8 °C and summer high of 29 °C. Dominant grasses are little bluestem (*Schizachyrium scoparium*) and indian grass (*Sorghastrum nuttans*), and dominant woody vegetation includes ashe juniper (*Juniperus ashei*) and live oak (*Quercus fusiformis*). The vegetation types on Fort Hood are mapped in Fig. 1.

Fort Bliss comprises a 282,500-ha military reserve in the northern Chihuahuan desert region of southern New Mexico. It has an arid climate with 255 mm of precipitation on average. With temperatures ranging between 2 and 35 °C. The vegetation is typical of the area surrounding the installation, consisting of perennial bunch grass and mat grasses such as sideoats grama (*Bouteloua curtipendula*), black grama (*Bouteloua eripoda*), hairy grama (*Bouteloua hirsuta*), and blue grama (*Bouteloua gracilis*). Figure 2 shows a map of vegetation types on Fort Bliss Fig. 2.

Fort Carson consists of 98,800 ha of training lands in southeastern Colorado. It receives 305 mm of annual precipitation on average and average temperatures are 1 °C in the winter and 24 °C in the summer. The vegetation on the training lands is typical for the region and comprised of shortgrass steppe or desert grasslands with shrublands and woodlands interspersed. Dominant grasses are blue grama (*Bouteloua gracilis*), black grama (*Bouteloua*

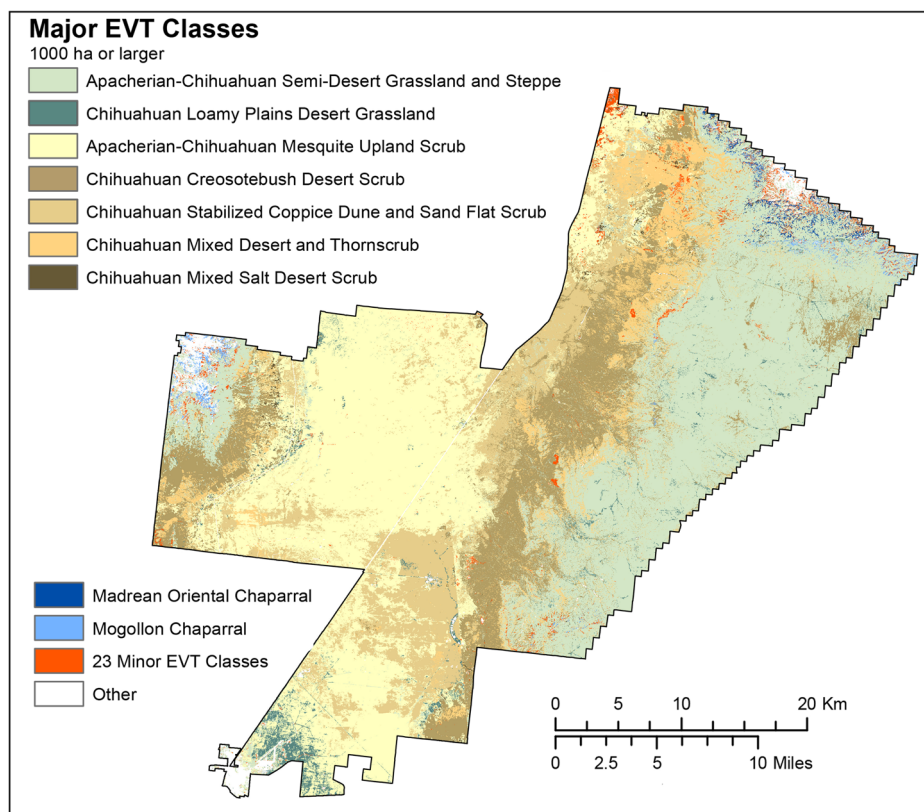


Fig. 2 Map of the major Landfire Existing Vegetation Types on Fort Bliss. Only those comprised of more than 100 ha are included. All others are included as “minor EVT classes.” Areas not classified by Landfire are labeled “other”

eripoda), and western wheatgrass (*Pascopyrum smithii*). Succulents such as cholla (*Opuntia imbricata*) and yucca (*Yucca glauca*) are also common. Figure 3 shows the distribution of vegetation types on Fort Carson.

The Fort Riley installation includes 40,273 ha of training area in the Flint Hill region of Kansas. It receives 835 mm of annual precipitation on average. The average low temperature is -3 and 27°C is the average high temperature. The vegetation on the training area is similar to that of the surrounding Flint Hills region consisting of tallgrass prairie with some woodlands and shrublands intermixed. Dominant grasses are big bluestem (*Andropogon gerardii*), indian grass (*Sorghastrum nuttans*), and switchgrass (*Panicum virgatum*). Dominant shrubs are buckbrush (*Symphoricarpos orbiculatas*) and smooth sumac (*Rhus glabra*). Vegetation types for Fort Riley are shown in Fig. 4.

Probabilities of falling outside the historical climate envelope for each vegetation type on each base were determined by calculating the proportion of grid cells in each vegetation type on a given installation falling outside of the historical climate envelope for that vegetation type under each future climate scenario. For this analysis, we held precipitation to historical levels while modeling annual average temperature increases of 1, 2, 3, 4, 5, 6, 7,

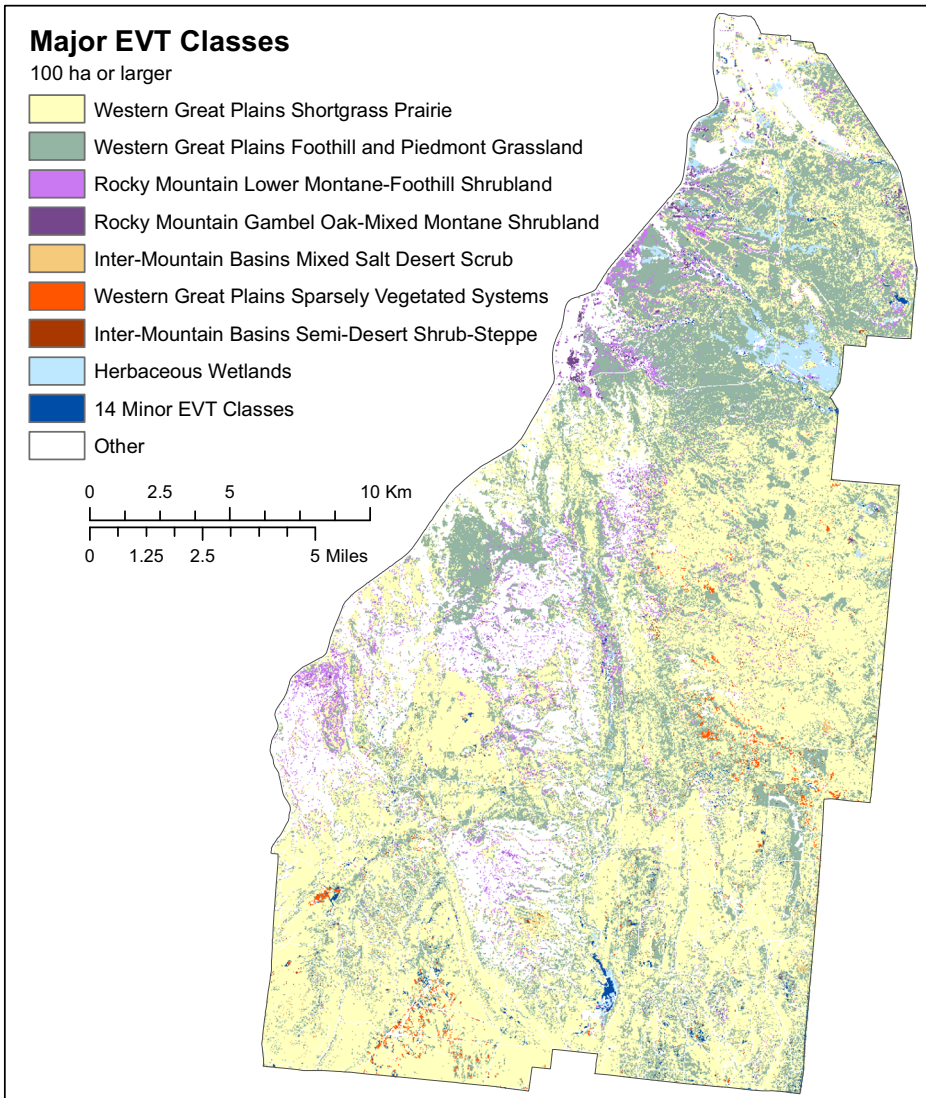


Fig. 3 Map of the major Landfire Existing Vegetation Types on Fort Carson. Only those comprised of more than 100 ha are included. All others are included as “minor EVT classes.” Areas not classified by Landfire are labeled “other”

8, 9, and 10 °C. This gradient of temperature corresponds with National Climate Assessment projected temperatures for the continental USA (Wuebbles et al. 2017). We chose a larger gradient in order to identify thresholds that occur at temperatures above National Climate Assessment projections. With this method, we were able to pinpoint the temperature increase that leads to a high likelihood of falling outside the historical climate envelope. We focused on temperature for the scenario analyses because separation between the

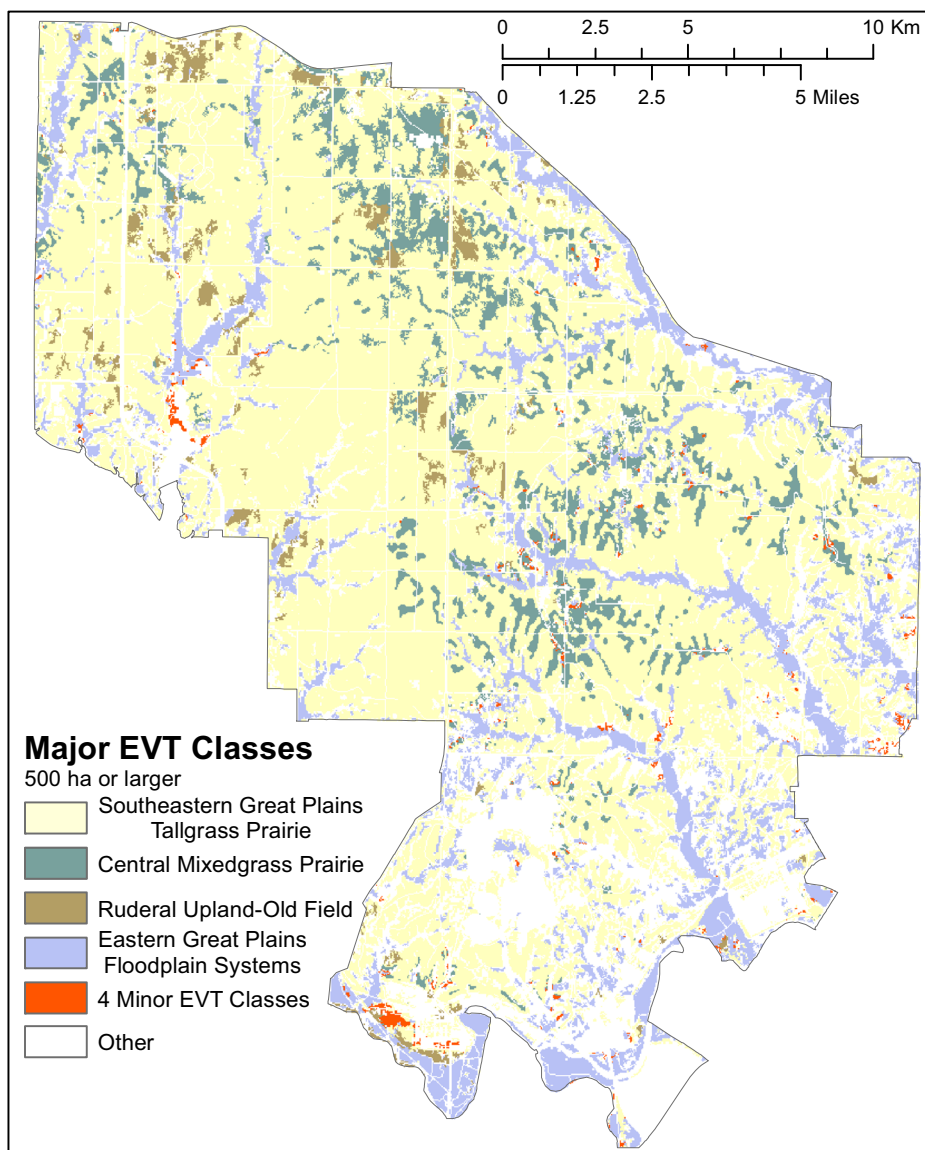


Fig. 4 Map of the major Landfire Existing Vegetation Types on Fort Carson. Only those comprised of more than 100ha are included. All others are included as “minor EVT classes.” Areas not classified by Landfire are labeled “other”

probability density plots for current and projected climate variables was more pronounced for temperature than precipitation for all of the vegetation types within the military installations. This single variable focus also provided more clarity for illustrative purposes. Managers could combine a scenario-based change in temperature with changes (both increases and decreases) in average annual precipitation or other climate-change variables to obtain a more nuanced view of the potential for climate-induced vegetation shifts.

3 Results

3.1 Relative vulnerability to state transitions among rangeland ecosystems of the continental USA

We mapped the Jaccard Dissimilarity Coefficient for each rangeland vegetation type identified by the existing vegetation-type landcover classification in order to identify hot spots sensitive to climate-induced vegetation changes. We show the climate vulnerability map using the HadleyCM3 A1 climate model (Fig. 5a) and the PCM B1 climate model (Fig. 5b).

This mapping approach can be repeated with any climate prediction model. Under the HadleyCM3 A1 climate model (higher sensitivity model), the northwestern Great Plains and Rocky Mountain regions, eastern Kansas, and large portions of central and western Texas show a very high likelihood of transitioning to alternative states due to climate change (Jaccard Index 0.9–1). Substantial portions of southwestern Arizona and areas in north central California, southeastern California, north central Arizona, and the central Great Plains show high likelihood of transition (Jaccard Index 0.6–0.7). There are additional small pockets of high and very high likelihood of transition across the southeastern USA and the eastern portion of the Pacific Northwest (Jaccard Index 0.6–1). Under the PCM B1 (lower sensitivity model), the most vulnerable vegetation types occur in western Texas and the southwestern USA. These areas show a very high likelihood of shifting to an alternative state due to climate change (Jaccard Index 0.91–1). A small region of southwestern California has a high likelihood of transition (Jaccard Index 0.61–0.7), and a portion of the vegetation types in the northwestern plains and rocky mountains show a moderate chance of transition (Jaccard Index 0.31–0.5). The majority of other areas have little potential to shift to alternative states with climate change (Jaccard Index < 0.2). The Jaccard Index value for each nonforested environment types in the continental USA is listed in the [Supporting Information S1](#).

Separation between the probability density plots for current and modeled climate variables was more pronounced for temperature than precipitation for most nonforested environment types under both the HadleyCM3 A1 climate model and the PCM B1 climate model (Example Fig. 6; HadleyCM3 model for all environment types see the [Supporting Information S2](#)).

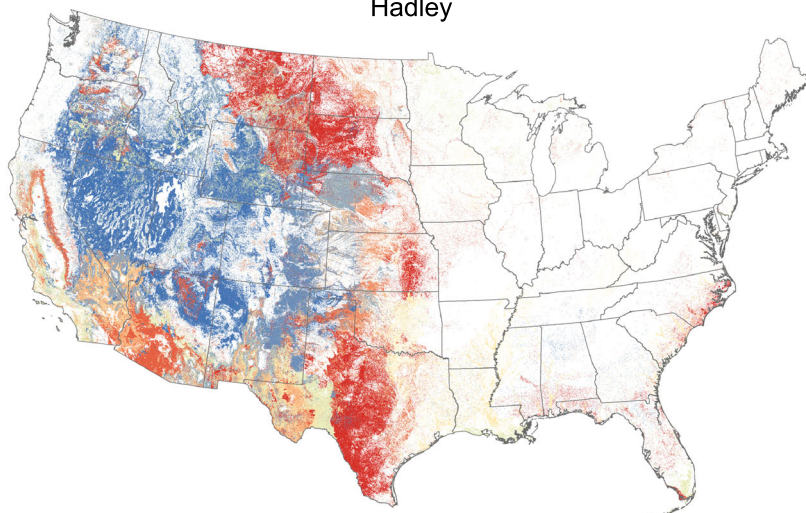
3.2 Site-specific ecosystem vulnerability to state transitions

All vegetation types at Fort Hood have a probability of 1 for falling outside of the historical climate envelope according to end-of-century climate projections with a 3 °C change in temperature (Table 1). The Edwards Plateau Dry Mesic Slope Forest is the most vulnerable to state change due to climate divergence, with a probability of falling outside historical climate of 1 at 2 °C. The Western Great Plains Mesquite Woodland and Shrubland vegetation type is also fairly vulnerable with a 0.6 probability of falling outside the historical climate envelope with a 2 °C change in temperature. Modified-Managed Southern Tall Grassland and Barren vegetation types are the least likely to fall outside historical climate envelopes. Probability of falling outside the climate envelope for each vegetation type at Fort Hood is shown in [Supporting Information S3](#).

Fort Bliss is less vulnerable to climate change than Fort Hood, with many of the vegetation types having zero probability of falling outside the historical climate envelope until there is greater than 5 °C temperature increase (Table 1). The Chihuahuan Stabilized Coppel Dune and Sand Flat Scrub is the most vulnerable to state shift from climate divergence

a)

Hadley



b)

PCM

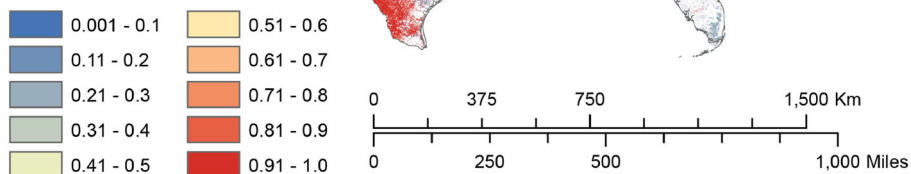
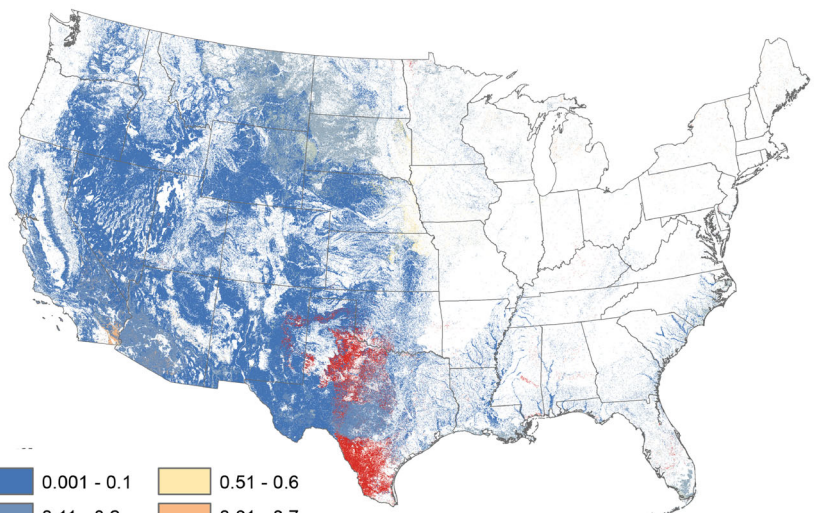


Fig. 5 Map of Jaccard Dissimilarity Coefficient for each non-forested vegetation type identified by the existing vegetation type landcover classification. Panel **a** shows the climate vulnerability map using the HadleyCM3 A1 climate model. Panel **b** shows the climate vulnerability map using PCM B1 climate model

with a probability of 0.25 of falling outside the climate envelope with a 3 °C increase in temperature. Probability of falling outside the climate envelope for each vegetation type at Fort Bliss is shown in [Supporting Information S3](#).

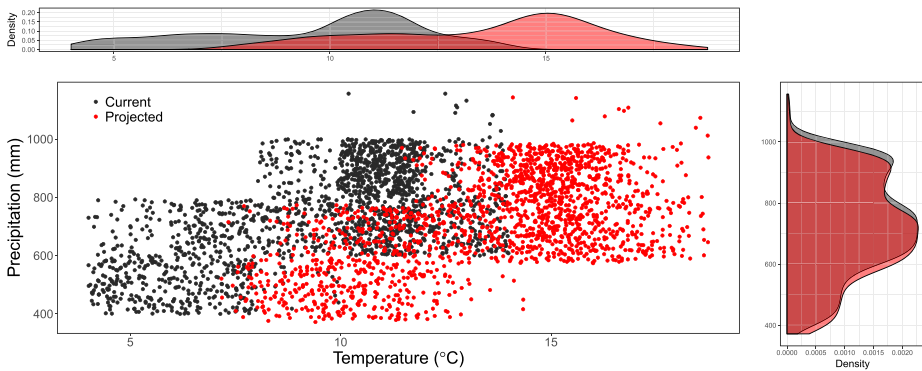


Fig. 6 Visual representations of potential for state change in vegetation types from the historical climate envelopes and predicted climates for grid cells. The center panel shows raw data (one point for each grid cell) plotted with mean annual average temperature on the *x*-axis and accumulated annual precipitation on the *y*-axis. Black points represent historical temperature and precipitation for grid cells and the red show the temperature and precipitation under the Hadley CM3 A1 projection for grid cells in a given environment type. The top panel plots a probability density function applied to temperature and shows the likelihood that average annual temperature takes a given value for each vegetation type under historical climate (black) and under end-of-century climate projections using the Hadley CM3 A1 climate model (red). The right-side panel plots a probability density function applied to precipitation and shows the likelihood that annual accumulated precipitation takes a given value for each vegetation type under historical climate (black) and under end-of-century climate projections using the Hadley CM3 A1 climate model (red). Figures for all nonforested vegetation types using the Hadley CM3 A1 climate model are provided in the [Supplemental Information](#)

Fort Riley has several vegetation types vulnerable to potential climate-induced state shifts (Table 1). The North Central Interior Dry Mesic Oak Forest and Woodland and the Eastern Great Plains Floodplain systems have a 0.75–1 probability of falling outside the historical climate envelope with a 2 °C increase in temperature. The other vegetation types at Fort Riley are not likely to fall outside the historical climate envelope until an increase in temperature of > 5 °C. Probability of falling outside the climate envelope for each vegetation type at Fort Riley is shown in [Supporting Information S3](#).

Fort Carson has only one vegetation type with a high probability of falling outside of the historical climate envelope with relatively minor increases in average annual temperature (Table 1). The Western Great Plains Foothill and Piedmont Grassland vegetation type has a 0.25 probability of falling outside the historical climate envelope with a 2 °C increase in temperature and a probability of 1 with an increase of 3 °C. The other vegetation types at Fort Carson fall within the historical climate envelope until the average annual temperature increases by > 4 °C. Probability of falling outside the climate envelope for each vegetation type at Fort Carson is shown in [Supporting Information S3](#).

4 Discussion

Under both climate scenarios, there is a very high likelihood of a vegetation shift in western and central Texas and southwestern Arizona. In addition, there is at least a moderate chance of vegetation shift in the northwestern plains and Rocky Mountains. This vulnerability occurs because of the high departure in these areas from the historical climate with little overlap between historical average envelope and end-of-century projections. Some areas such as

Table 1 Change in temperature (°C) that results in a probability of 1.00 for each vegetation type on each military installation

Existing vegetation type (by installation)	Change in temperature (°C)
Fort Hood	
Barren	6
Western Great Plains Mesquite Woodland and Shrubland	3
Western Great Plains Floodplain Systems	3
Edwards Plateau Limestone Savanna and Woodland	3
Edwards Plateau Limestone Shrubland	3
Edwards Plateau Dry Mesic Slope Forest and Woodland	2
Modified-Managed Southern Tall Grassland	5
Fort Bliss	
Barren	9
Southern Rocky Mountain Pinyon-Juniper Woodland	7
Chihuahuan Creosotebush Desert Scrub	6
Chihuahuan Stabilized Coppice Dune and Sand Flat Scrub	4
Apacherian-Chihuahuan Mesquite Upland Scrub	7
Chihuahuan Mixed Desert and Thornscrub	7
Madrean Oriental Chaparral	7
Mongollon Chaparral	7
Apacherian-Chihuahuan Semidesert Grassland and Steppe	9
Chihuahuan Loamy Plains Desert Grassland	2
Chihuahuan-Sonoran Desert Bottomland and Swale Grassland	2
Fort Riley	
Central Mixedgrass Prairie	7
North Central Dry Mesic Oak Forest and Woodland	3
Southeastern Great Plains Tallgrass Prairie	6
Eastern Great Plains Floodplain Systems	4
Ruderal Upland-Old Field	More than 10
Fort Carson	
Herbaceous Wetlands	More than 10
Rocky Mountain Lower Montane-Foothill Shrubland	8
Southern Rocky Mountain Pinyon-Juniper Woodland	9
Southern Rocky Mountain Pondersosa Pine Woodland	5
Western Great Plains Foothill and Piedmont Grassland	3
Western Great Plains Shortgrass Prairie	10

the upper Northern Plains, the Flint Hills region of the Great Plains, and central Texas are highly vulnerable to state shift when the Hadley CM3 A1 global circulation model is used, but show low vulnerability under the PCM B1 model. More areas are vulnerable under the Hadley model because this model is characterized by a large increase in temperatures and reduction in precipitation resulting from continued high fossil fuel emissions, while the PCM model is characterized by a smaller increase in temperature and smaller reduction in precipitation as a result of future reductions in emissions. This difference highlights an important outcome of our approach. There is a great amount of uncertainty in modeling the

interaction among oceanic, atmospheric, and cryospheric components of global circulation (Cess et al. 1990). Different parameterizations of climate feedbacks and processes results in different predictions for end-of-century climate envelopes. Our approach allows for the identification of areas that are determined to be highly vulnerable across multiple global circulation models. Additionally, vulnerability maps can be updated as global circulation models are further refined.

Vegetation types identified as highly vulnerable across multiple global circulation models are more likely to be exposed to combinations of climatic variables that are different from those under which they evolved. This can lead to modification of interspecific interactions within and across trophic levels with the potential for those altered interactions to result in large shifts in vegetation community composition, structure, and function (Lawler 2009; Walther et al. 2002). For instance, postglacial climate change is thought to have driven the formation of novel plant communities as a result of changes in plant-herbivore interactions and the new vegetation structure contributed to altered disturbance regimes (e.g., fire) which reinforced the persistence of newly established plant communities (Gill et al. 2009). Similar shifts could occur for vegetation types identified as vulnerable in our study. There is also indication from contemporary studies that climate change alters plant community interactions and may again lead to novel assemblages (Gilman et al. 2010; Klanderud 2005) with unique reinforcing processes and functions. Reassembly is likely due to the strong influence of climate on community structuring processes (e.g., plant species distributions), interspecific interactions (e.g., facilitation and increased competition), disturbance regimes, and meta-community processes (e.g., dispersal and migration) (Brooker et al. 2008; Callaway et al. 2002; Callaway and Aschehoug 2000; Gilman et al. 2010). Novel assemblages could lead to shifts in dominance as species that have not co-evolved begin to coexist (Callaway and Aschehoug 2000), and novel feedbacks emerge that maintain the novel species compositions over time (Brooker et al. 2008; Gill et al. 2009).

This potential for climate-induced shifts in species assemblages and the processes and functions that maintain them is especially concerning in rangeland ecosystems. Rangelands provide important ecosystem services worldwide, with large portions of the global human population relying on them for livelihoods, food, clean water, and cultural services associated with biodiversity (Havstad et al. 2007). When faced with perturbations such as climate alteration and attendant changes in disturbance regimes, nonforested systems have been shown to be prone to reaching ecosystem tipping points—abrupt transitions in ecosystem composition and structure that result in a switch to an alternative ecosystem state (Yang et al. 2011). These shifts are difficult to reverse because they occur concurrently with fundamental shifts in self-reinforcing feedbacks that maintain the system in a given state (Grimm et al. 2013; Higgins and Harte 2012). Often, these state shifts are accompanied by a shift in the type of ecosystem services provided. This can be problematic for people who have become dependent upon the services previously provided. Therefore, a key management objective for rangeland systems is avoiding tipping points and state transitions in order to maintain the provision of ecosystem services that people rely upon in these systems (Bestelmeyer et al. 2004). Identifying where state shifts are more likely to occur could assist managers in prioritizing limited mitigation and adaptation resources.

With the average global temperature expected to increase by 1.1 to 6.4 °C and precipitation patterns worldwide projected to change dramatically by the end-of-the century (Lawler 2009), managing rangelands away from tipping points and preventing shifts toward less productive systems will become increasingly difficult. Resources and manpower for adapting to climate change are limited and will become increasingly so as climate effects manifest more strongly. In order to avoid potentially harmful state shifts, managers need

a means for prioritizing limited climate-adaptation resources; however, climate vulnerability analyses for nonforested ecosystems useful for identifying areas where climate change is most likely to lead to state shifts are lacking. Vulnerability analyses previously available for rangelands either focus on the vulnerability of a particular ecosystem service, such as rancher/pastoralist livelihood (Hanson et al. 1993, see, e.g., Martin et al. 2014) or net primary productivity (Reeves et al. 2014, see, e.g.,), or looked at the vulnerability of a specific area in depth (Christensen et al. 2004, see, e.g., Dougill et al. 2010; Volder et al. 2013) without providing a relative contrast to other rangelands. Those analyses that explore relative vulnerability and could therefore provide utility for prioritizing climate-adaptation resources have focused solely on climate exposure of rangelands (Briske et al. 2015, see, e.g., Joyce et al. 2013; Polley et al. 2013). This focus on exposure alone ignores the potential for differential impacts at a specific level of exposure among different community types.

Our approach provides an integrated measure of exposure and sensitivity that can be used to determine the relative vulnerability of rangelands to climate-induced state shifts. Our vulnerability index and the smaller scale scenario analyses incorporate the ranges of climate across current vegetation types (as classified by the LANDFIRE evt database) as a measure of sensitivity, and tie exposure to sensitivity by determining potential climatic divergence across the entire range for that vegetation community. Communities classified by LANDFIRE existing vegetation types represent a group of plant community types that tend to co-occur within landscapes with similar ecological processes, substrates, and environmental gradients (Comer et al. 2003). Because of their focus on community structuring processes as an underpinning for the classification system, LANDFIRE existing vegetation types have been useful in a range of applications including assessments of habitat and wildlife relationships (Chaplin-Kramer et al. 2011; Gnass Giese et al. 2015; Olson et al. 2014), developing indicators of ecological condition (Wang et al. 2010), and in determining plant phenological response to climate change (Meier et al. 2015). Thus, they provide detailed information on vegetation-type distributions based on plant traits and the processes driving community assembly. As a result, they reflect the tolerance of dominant vegetation in the community to climatic and environmental filters (Rollins 2009), making them more robust proxies of vegetation community sensitivity than other landcover classification systems. One limitation to our approach, however, is that it does not address the third element of vulnerability—adaptive capacity (Smit and Wandel 2006). Policy-makers who wish to determine relative vulnerability in a more socioeconomic context will also need to consider the ability for different rangeland managers to undertake adaptation.

One advantage of our approach to prioritization at the broad scale is that the index can be used with any existing climate-forcing models and therefore updated as new models are developed. While we used the PCM B1 and HadleyCM3 A1 to represent the extremes of possible outcomes (Iverson et al. 2008), new climate models are constantly being developed and previous ones updated. While this provides challenges to consistency in determining management priorities, a relative metric such as ours lowers the potential that new models will lead to vastly different priority rankings. While there was some divergence in magnitude of vulnerability for a given location between the two climate models, the index consistently identified several areas as highly vulnerable to an ecosystem-state transition under future global climate change and the relative vulnerability pattern was fairly consistent across models. This would likely not be the case with a more mechanistic approach to determining vulnerability. For instance, dynamic global vegetation models (DGVMs) that provide a mechanistic link between plant functional types and climate drivers of distribution require more climate variable inputs (Sitch et al. 2003, e.g., minimum coldest month temp, number of growing season days, etc.), and are therefore prone to divergence when employing

different climate-forcing models. These more mechanistic models also increase the potential for erroneous prioritization because they require a representation of the complex processes that lead to community compositional shift under changing climate. As a result, the many different DGVMs have resulted in widely divergent predictions even when parameterized with the same inputs (Cramer et al. 2001). Therefore, a simpler scheme for prioritizing areas for concern under a changing climate can help target more detailed analyses aimed at determining how vegetation might change in the future, such as DGVMs.

While a relative index based on climate projections is appropriate at broad scales (i.e., national), where prioritization must occur immediately in the face of incomplete knowledge, at smaller scales (i.e., individual management units), there is often a need to evaluate vulnerability across a range of potential future climate conditions. Local needs and capabilities regarding climate-change adaptation differ from those at larger scales (Wilbanks and Kates 1999). Managers of individual land units can move more cautiously because they are able to react more quickly to changing conditions than are national land-management agencies. Therefore, a scenario planning approach is more appropriate at the smaller scale, where managers armed with information regarding vulnerability to thresholds under a range of climate scenarios can plan accordingly while attempting to discern the likely future climate trajectory for their site. Indices based on climate-forcing models are less reliable at this scale, as the error in climate-forcing models increases substantially as they are scaled down.

At all four Department of Defense installations that served as examples for small-scale vulnerability analysis, some vegetation types emerged as more vulnerable than others at low levels of departure from current temperatures, with those differences in vulnerability decreasing as departure increases. These types of scenario analyses provide a better understanding of uncertainty with regards to predicted responses to climate change and therefore contribute to the development of climate-adaptation at local scales that is responsive to a wide range of potential future climates (Moss et al. 2010). In addition, small-scale analyses can incorporate additional variables such as maximum temperatures, frequency of extreme events such as droughts and floods, and increasing evening temperatures as those types of variables could be more important to vegetation dynamics than average annual temperature and precipitation in some ecosystems (Niu et al. 2014). The degree of nuance in scenario analyses should reflect the level of understanding of climate-change effects on ecosystem processes for a given land holding.

Several limitations of climate envelope approaches such as ours require them to be coupled with more mechanistic models to accurately predict outcomes of vegetation shifts. For instance, climate envelope models represent a realized niche, rather than a fundamental niche, and therefore might be prone to underestimating climates where plants can live. In addition, in a no-analogue future, where the sets of interacting species potentially change, barriers stopping species from realizing their fundamental niche could be lessened, allowing species to potentially persist in locations that currently appear outside their climate envelopes. Furthermore, while climate change is an important driver of state shifts in rangelands and interacts with other drivers often even when it is not the proximate driver (Rocha et al. 2015), it is not the only driver of state shifts. There are many other factors that could increase the likelihood of state shift in an area where climatic change is not a major concern (Scheffer et al. 2001; Bestelmeyer et al. 2015).

One potential global change-related driver of vegetation community dynamics that is not included in our analysis is CO₂ enrichment and its interaction with warming. Long-term experiments show community shifts under elevated CO₂ and warming to be extremely dynamic (Mueller et al. 2016; Zelikova et al. 2015). Studies have shown increases in an

invasive forb (Blumenthal et al. 2013), a short-term shift to C4 grass dominance that was diminished over time (Mueller et al. 2016), and other temporally dynamic community compositional shifts (Zelikova et al. 2014; De Kauwe et al. 2017). Disentangling the myriad interacting drivers and directions of compositional shift requires long-term multifactor experiments, which are costly and logistically difficult to carry out (De Kauwe et al. 2017). Effects of warming and elevated CO₂ have been shown to be even more temporally variable in semiarid grasslands because of the interaction of these climate-change variables with precipitation and other variables such as grazing type and pressure (Mueller et al. 2016; Augustine et al. 2018).

Given all the interacting variable that contribute to community compositional dynamics and state shifts, more mechanistic models of plant community response to future changes in climate characteristics are important to the development of specific adaptation measures and effective management as they provide a detailed look at potential future vegetation configurations on the landscape (Wise et al. 2014). These types of models require intensive data inputs and a detailed understanding of community assembly mechanisms that often must be derived from empirical experimentation (Williams and Jackson 2007). It is often not possible to obtain these detailed data across all of the communities that a management entity is responsible for. Therefore, a more simplistic, relative approach to determining potential vulnerability such as the one outlined here is essential to identifying areas where the need for more mechanistic modeling is most urgent.

Ultimately, with 60% of ecosystem services already lost to human activity (IPCC 2007), the focus of prioritization will increasingly lean toward protecting the suite of ecosystem services desired from a region regardless of ecosystem state shifts. However, this is a difficult undertaking as it requires working knowledge of the processes that result in those desired services, the development of an system for identifying services provided by each ecosystem, and a way to value competing services (Mooney et al. 2009). While our approach does not specifically address this, regime shifts often lead to a loss of desired ecosystem services (Scheffer et al. 2001; Mäler 2000). Given this, our approach can serve as a basis for precautionary prioritization until a more complete understanding of climate-change effects on ecosystem services provides opportunity for developing a prioritization scheme specifically aimed at maximizing ecosystem service delivery.

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References

- Augustine DJ, Blumenthal DM, Springer TL, LeCain DR, Gunter SA, Derner JD (2018) *Ecol Appl* 28(3):721
- Bestelmeyer BT (2006) *Restoration Ecology* 14(3):325. <https://doi.org/10.1111/j.1526-100X.2006.00140.x>, <http://onlinelibrary.wiley.com.lib-ezproxy.tamu.edu:2048/doi/10.1111/j.1526-100X.2006.00140.x/abstract>
- Bestelmeyer BT, Herrick JE, Brown JR, Trujillo DA, Havstad KM (2004) *Environmental Management* 34(1):38. <https://doi.org/10.1007/s00267-004-0047-4>, <http://link.springer.com.lib-ezproxy.tamu.edu:2048/article/10.1007/s00267-004-0047-4>

- Bestelmeyer BT, Okin GS, Duniway MC, Archer SR, Sayre NF, Williamson JC, Herrick JE (2015) *Front Ecol Environ* 13(1):28
- Blumenthal DM, Resco V, Morgan JA, Williams DG, LeCain DR, Hardy EM, Pendall E, Bladyka E (2013) *New Phytol* 200(4):1156
- Briske DD, Fuhlendorf SD, Smeins FE (2006) *Rangel Ecol Manag* 59(3):225. <http://www.jstor.org.lib-ezproxy.tamu.edu/2048/stable/3899924>
- Briske DD, Joyce LA, Polley HW, Brown JR, Wolter K, Morgan JA, McCarl BA, Bailey DW (2015) *Front Ecol Environ* 13(5):249
- Brooker RW, Maestre FT, Callaway RM, Lortie CL, Cavieres LA, Kunstler G, Liancourt P, Tielbörger K, Travis JM, Anthelme F (2008) *J Ecol* 96(1):18
- Callaway RM, Aschehoug ET (2000) *Science* 290(5491):521
- Callaway RM, Brooker R, Choler P, Kikvidze Z, Lortie CJ, Michalet R, Paolini L, Pugnaire FI, Newingham B, Aschehoug ET (2002) *Nature* 417(6891):844
- Cess RD, Potter G, Blanchet J, Boer G, Del Genio A, Deque M, Dymnikov V, Galin V, Gates W, Ghan S et al (1990) *J Geophys Res-Atmos* 95(D10):16601
- Chaplin-Kramer R, Tuxen-Bettman K, Kremen C (2011) *Rangelands* 33(3):33
- Christensen L, Coughenour MB, Ellis JE, Chen ZZ (2004) *Clim Chang* 63(3):351
- Clark JS, Bell DM, Hersh MH, Nichols L (2011) *Glob Chang Biol* 17(5):1834
- Comer P, Faber-Langendoen D, Evans R, Gawler S, Josse C, Kittel G, Menard S, Pyne M, Reid M, Schulz K (2003) *Natureserve*, Arlington VA
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD (2001) *Glob Chang Biol* 7(4):357
- De Kauwe MG, Medlyn BE, Walker AP, Zaehle S, Asao S, Guenet B, Harper AB, Hickler T, Jain AK, Luo Y et al (2017) *Glob Chang Biol* 23(9):3623
- Dougill AJ, Fraser EDG, Reed MS (2010) Anticipating vulnerability to climate change in dryland pastoral systems: using dynamic systems models for the Kalahari. *Ecol Soc* 15(2):17
- Füssel HM (2007) *Glob Environ Chang* 17(2):155
- Füssel HM (2010) Review and quantitative analysis of indices of climate change exposure, adaptive capacity, sensitivity, and impacts (Washington DC: World Bank
- Füssel HM, Klein RJ (2006) *Clim Chang* 75(3):301
- Gill JL, Williams JW, Jackson ST, Lininger KB, Robinson GS (2009) *Science* 326(5956):1100
- Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) *Trends Ecol Evol* 25(6):325
- Gnass Giese EE, Howe RW, Wolf AT, Miller NA, Walton NG (2015) *Ecosphere* 6(6):1
- Gonzalez P, Neilson RP, Lenihan JM, Drapek RJ (2010) *Glob Ecol Biogeogr* 19(6):755
- Grimm NB, Chapin FS, Bierwagen B, Gonzalez P, Groffman PM, Luo Y, Melton F, Nadelhoffer K, Pairis A, Raymond PA (2013) *Front Ecol Environ* 11(9):474
- Hanson J, Baker B, Bourdon R (1993) *Agric Syst* 41(4):487
- Havstad KM, Peters DP, Skaggs R, Brown J, Bestelmeyer B, Fredrickson E, Herrick J, Wright J (2007) *Ecol Econ* 64(2):261
- Heikkinen RK, Luoto M, Araújo MB, Virkkala R, Thuiller W, Sykes MT (2006) *Prog Phys Geogr* 30(6):751
- Higgins PA, Harte J (2012) *J Clim* 25(21):7660
- IPCC A (2007) *Climate change 2007: synthesis report*
- Iverson L, Prasad A, Matthews S (2008) *Mitig Adapt Strateg Glob Chang* 13(5-6):487
- Jaarsveld ASV, Freitag S, Chown SL, Muller C, Koch S, Hull H, Bellamy C, Krüger M, Endrödy-Younga S, Mansell MW, Scholtz CH (1998) *Science* 279(5359):2106. <https://doi.org/10.1126/science.279.5359.2106>. <http://www.sciencemag.org/content/279/5359/2106>
- Joyce LA, Briske DD, Brown JR, Polley HW, McCarl BA, Bailey DW (2013) *Rangel Ecol Manag* 66(5):512
- Klanderud K (2005) *J Ecol* 93(1):127
- Lawler JJ (2009) *Ann N Y Acad Sci* 1162(1):79
- Leemans R, Eickhout B (2004) *Glob Environ Chang* 14(3):219
- Mäler KG (2000) *Eur Econ Rev* 44(4-6):645
- Martin R, Müller B, Linstädter A, Frank K (2014) *Glob Environ Chang* 24:183
- Meier GA, Brown JF, Ewelsizer RJ, Vogelmann JE (2015) *Ecol Indic* 48:189
- Mooney H, Larigauderie A, Cesario M, Elmquist T, Hoegh-Guldberg O, Lavorel S, Mace GM, Palmer M, Scholes R, Yahara T (2009) *Curr Opin Environ Sustain* 1(1):46
- Moss RH, Edmonds JA, Hibbard KA, Manning MR, Rose SK, Van Vuuren DP, Carter TR, Emori S, Kainuma M, Kram T (2010) *Nature* 463(7282):747
- Mueller KE, Blumenthal DM, Pendall E, Carrillo Y, Dijkstra FA, Williams DG, Follett RF, Morgan JA (2016) *Ecol Lett* 19(8):956
- Niu S, Luo Y, Li D, Cao S, Xia J, Li J, Smith MD (2014) *Environ Exp Bot* 98:13

- Olson LE, Sauder JD, Albrecht NM, Vinkey RS, Cushman SA, Schwartz MK (2014) *Biol Conserv* 169:89
- Polley HW, Briske DD, Morgan JA, Wolter K, Bailey DW, Brown JR (2013) *Rangel Ecol Manag* 66(5):493
- Preston BL, Yuen EJ, Westaway RM (2011) *Sustain Sci* 6(2):177
- Randall DA, Wood RA, Bony S, Colman R, Fichet T, Fyfe J, Kattsov V, Pitman A, Shukla J, Srinivasan J (2007) In: *Climate change 2007: the physical science basis. Contribution of working group I to the fourth assessment report of the IPCC (FAR)* (Cambridge University Press), pp 589–662
- Reeves MC, Moreno AL, Bagne KE, Running SW (2014) *Clim Chang* 126(3–4):429
- Rocha JC, Peterson GD, Biggs R (2015) *PLoS One* 10(8):e0134639
- Rollins MG (2009) *Int J Wildland Fire* 18(3):235
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) *Nature* 413(6856):591
- Silverman BW (1986) *Density estimation for statistics and data analysis*. Routledge, Abingdon
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W, Sykes MT (2003) *Glob Chang Biol* 9(2):161
- Smit B, Wandel J (2006) *Glob Environ Chang* 16(3):282
- Stein BA, Scott C, Benton N (2008) *BioScience*. 58(4). <https://doi.org/10.1641/B580409>, bib-tex[eprint=/oup/backfile/content_public/journal/bioscience/58/4/10.1641_b580409/4/58-4-339.pdf]
- Tazik DJ, Martin CO (2002) *Arid Land Res Manag* 16(3):259
- Thuiller W (2004) *Glob Chang Biol* 10(12):2020
- Vincent CH, Hanson LA, Argueta CN (2017) *Federal land ownership: overview and data*. Congressional research, service report R42346
- Volder A, Briske DD, Tjoelker MG (2013) *Glob Chang Biol* 19(3):843
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) *Nature* 416(6879):389
- Wang Y, Nemani R, Dieffenbach F, Stolte K, Holcomb G, Robinson M, Reese CC, Reese M, Duhaime R, Tierney G et al (2010) 2010 IEEE International Geoscience and Remote Sensing Symposium (IGARSS). (IEEE), pp 2095–2098
- Watson JE, Iwamura T, Butt N (2013) *Nat Clim Chang* 3(11):989
- Wilbanks TJ, Kates RW (1999) *Clim Chang* 43(3):601
- Williams JW, Jackson ST (2007) *Front Ecol Environ* 5(9):475
- Wise R, Fazey I, Smith MS, Park S, Eakin H, Van Garderen EA, Campbell B (2014) *Glob Environ Chang* 28:325
- Wuebbles D, Fahey D, Hibbard K, Dokken B, Stewart B, Maycock T (2017) In: *Washington, DC*, p 470
- Yang H, Wu M, Liu W, Zhang Z, Zhang N, Wan S (2011) *Glob Chang Biol* 17(1):452. <https://doi.org/10.1111/j.1365-2486.2010.02253.x>
- Zelikova TJ, Blumenthal DM, Williams DG, Souza L, LeCain DR, Morgan J, Pendall E (2014) *Proc Natl Acad Sci* 111(43):15456
- Zelikova TJ, Williams DG, Hoenigman R, Blumenthal DM, Morgan JA, Pendall E (2015) *J Ecol* 103(5):1119

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