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RESEARCH ARTICLE

Climate change and ecosystem composition across large landscapes

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Abstract

Context Climate change alters the vegetation composition and functioning of ecosystems. Measuring the magnitude, direction, and rate of changes in vegetation composition induced by climate remains a serious and unmet challenge. Such information is required for a predictive capability of how individual ecosystem will respond to future climates.

Objectives Our objectives were to identify the relationships between 20 climate variables and 39 ecosystems across the southwestern USA. We sought to understand the magnitude of relationships between variation in vegetation composition and bioclimatic variables as well as the amount of ecosystem area expected to be affected by future climate changes.

Methods Bioclimatic variables best explaining the plant species composition of each ecosystem were identified. The strength of relationships between beta turnover and bioclimate gradients was calculated, the spatial concordance of ecosystem and bioclimate configurations was shown, and the area of suitable climate remaining within the boundaries of contemporary ecosystems under future climate projections was measured.

Results Across the southwestern USA, four climate variables account for most of the climate related variation in vegetation composition. Twelve ecosystems are highly sensitive to climate change. By 2070, two ecosystems lose about 4000 (15 %) and 7000 (31 %) km^2 of suitable climate area within their current boundaries (the Western Great Plains Sandhill Steppe and Sonora-Mojave Creosotebush-White Bursage Desert Scrub ecosystems, respectively). The climatic areas of riparian ecosystems are expected to be reduced by half.

Conclusions Results provide specific climate and vegetation parameters for anticipating how, where and when ecosystem vegetation transforms with climate change. Projecting the loss of suitable climate for the vegetation composition of ecosystems is important for assessing ecosystem threats from climate change and for setting priorities for ecosystem conservation and restoration across the southwestern USA.

Keywords Terrestrial ecosystems · Climate change · Vegetation composition · Large area landscapes · Southwest USA · Bioclimate

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Introduction

Typically, scientific applications relying on climate change projections focus on average temperatures (Hare and Meinshausen 2006). While averages help with understanding generalized climatic changes, they tell little about how, where and when ecosystem properties, such as the composition of vegetation, respond to climate change. Some predictions of biotic responses to climate rely on envelope models (Pearson and Dawson 2003). While substantial work and debate focuses on bioclimate envelope modeling to predict species distributions (Busby 1991; Pearson and Dawson 2003; Elith and Leathwick 2009; Dainese 2012), few studies explore the issue of compositional responses of ecosystems to climate change, particularly at the floristic level (Baselga and Araújo 2009; Pucko et al. 2011; Friggens et al. 2012). Halpin (1997) showed that when the envelope of climatic conditions describing the distribution of an ecosystem no longer exists at a location, the ecosystem contracts and eventually disappears. Until a clear systematic basis for providing such information is developed, landscape scale ecosystems will remain rather amorphous entities: challenging to define, threats upon them hard to assess, and their ecological planning relegated to simply acknowledging that changes will happen. Without appropriate information, it will be difficult to predict specific landscape level outcomes or prepare adaptive management responses.

We address these issues by identifying relationships between the vegetation composition of ecosystems and bioclimatic variables. Our methods and results predict: (a) which ecosystems are most sensitive to changes of climate at the level of community composition, (b) the compositional direction of changes in vegetation that is likely to result, (c) the potential amount of area affected, and (d) potential magnitude of change. We focus on 39 ecosystems within the Southwest region of the USA (Fig. 1). Bioclimate is that set of climate variables which best explain the distribution of a given species or community, to the extent that climate influences its occurrence and make-up per se (Table 1). Our methods identify which bioclimatic variables best explain vegetation composition at local scales (~ 1 km^2). This process characterizes the principal vegetation related climatic properties of defined ecosystem types.

Subsequently, changes in vegetation composition along the primary bioclimate gradients of the ecosystems are quantified. We show the spatial expression of these gradients in relation to ecosystem occurrence. These relationships are then coupled with climate projections for the 2030s, 2050s and 2070s (Ramirez and Jarvis 2008; Donner et al. 2011), revealing the location, type and pace of projected ecosystem change. Effects of climate change are also assessed by measuring the area of suitable climate remaining within the boundaries of contemporary ecosystems under future climate projections. The procedure describes how the patterns of future climate across an ecosystem's current area are expected to differ from that which is suitable for its current composition. It offers more than a simple boundary shift model, as changes may occur anywhere within an ecosystem. This is important because, for instance, landscape fragmentation metrics can then be derived, yielding a more thorough understanding of how climate change is likely to alter spatial patterns of habitat at the patch scale of land management.

Methods

Our approach relies on observed relationships between the plant species composition of defined ecosystems and climate variables (Fig. 2).

We began by identifying the minimum least correlated set of bioclimatic variables that best explain the plant species composition of each ecosystem. Beta turnover (Tuomisto 2010) of the cline occurring across the bioclimate gradients of these ecosystems was quantified in order to measure the relationship between bioclimate and the composition of plant species across these ecosystems (Whittaker 1967). Then we identified places on the landscape where the bioclimate gradient is steep or gradual, indicating where the magnitude of climate forcing on these ecosystems is stronger or weaker across the landscape, given the continuous variation of bioclimate values over space and time. Lastly, within the boundaries of the ecosystems having the strongest composition-bioclimate relationships we calculated the amount of area projected into the 2030s, 2050s, and 2070s that is expected to retain the same range of bioclimate values in the future as the contemporary normals. This approach enables us to describe the amount of each

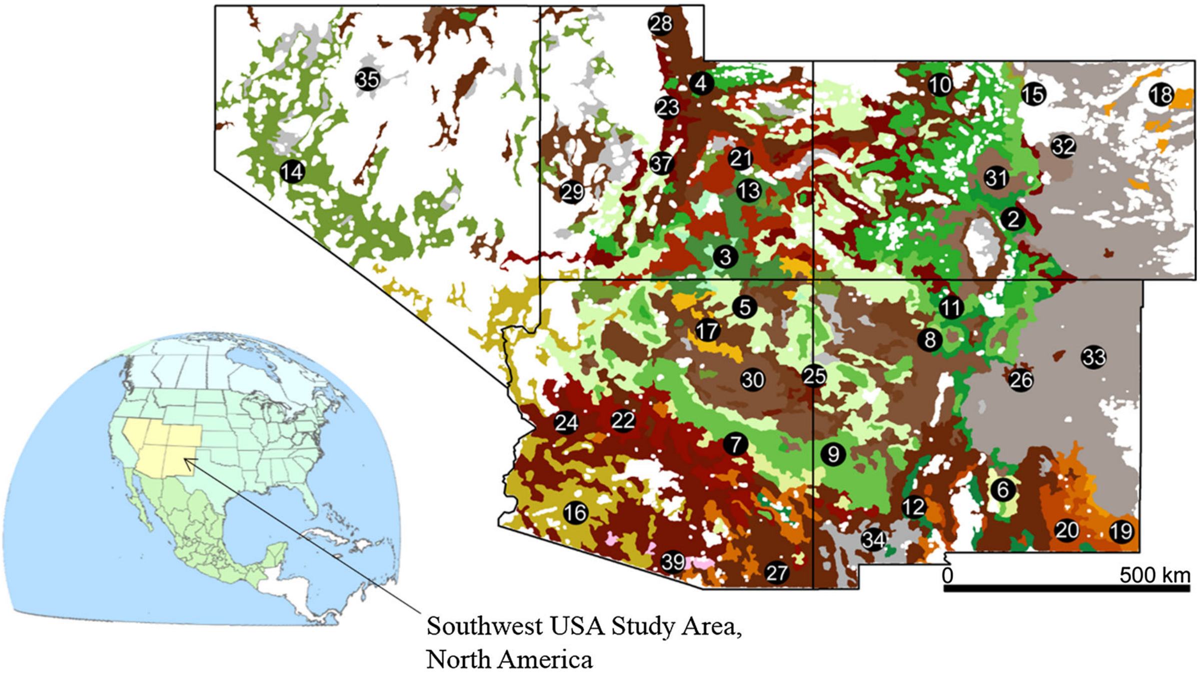

Fig. 1 Generalized distributions of the 39 ecosystems across the southwestern USA. Numbers indicate the following ecosystems, based on the U.S. National Vegetation Classification Group level names (Ecological Society of America et al. 2015). *1* Rocky Mountain Cliff, Canyon and Massive Bedrock; *2* Inter-Mountain Basins Active and Stabilized Dune; *3* Colorado Plateau Mixed Bedrock Canyon and Tableland; *4* Rocky Mountain Aspen Forest and Woodland; *5* Colorado Plateau Pinyon-Juniper Woodland; *6* Madrean Lower Montane Pine-Oak Forest and Woodland; *7* Madrean Pinyon-Juniper Woodland; *8* Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland; *9* Southern Rocky Mountain Ponderosa Pine Woodland; *10* Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland; *11* Southern Rocky Mountain Pinyon-Juniper Woodland; *12* Chihuahuan Creosotebush Desert Scrub; *13* Colorado Plateau Blackbrush-Mormon-tea Shrubland; *14* Inter-Mountain Basins Mixed Salt Desert Scrub; *15* Rocky Mountain Lower Montane-Foothill Shrubland; *16* Sonora-Mojave Creosotebush-White Bursage Desert Scrub; *17* Southern Colorado Plateau Sand Shrubland; *18* Western Great Plains Sandhill Steppe; *19* Apacherian-Chihuahuan Mesquite Upland Scrub; *20* Chihuahuan Mixed Desert and Thorn Scrub; *21* Colorado Plateau Pinyon-Juniper Shrubland; *22* Mogollon Chaparral; *23* Rocky Mountain Gambel Oak-Mixed Montane Shrubland; *24* Sonoran Paloverde-Mixed Cacti Desert Scrub; *25* Inter-Mountain Basins Juniper Savanna; *26* Southern Rocky Mountain Juniper Woodland and Savanna; *27* Apacherian-Chihuahuan Semi-Desert Grassland and Steppe; *28* Inter-Mountain Basins Montane Sagebrush Steppe; *29* Inter-Mountain Basins Semi-Desert Shrub-Steppe; *30* Inter-Mountain Basins Semi-Desert Grassland; *31* Southern Rocky Mountain Montane-Subalpine Grassland; *32* Western Great Plains Foothill and Piedmont Grassland; *33* Western Great Plains Shortgrass Prairie; *34* Chihuahuan Loamy Plains Desert Grassland; *35* Inter-Mountain Basins Greasewood Flat; *36* North American Warm Desert Wash; *37* Rocky Mountain Lower Montane-Foothill Riparian Woodland and Shrubland; *38* North American Warm Desert Lower Montane Riparian Woodland and Shrubland; *39* North American Warm Desert Riparian Woodland and Shrubland. Ecosystem numbers *1*, *36*, and *38* are absent from the map, given the coarse map scale and resolution. Geographic data of ecosystems are from NatureServe (2009)

ecosystem's area where the climate is expected to change beyond its contemporary range of variation.

Study area

We examined 39 ecosystems spanning the southwestern USA (Fig. 1). Comer et al. (2003) described these ecosystems and the USGS Gap Analysis Program (Prior-Magee et al. 2007) as well as NatureServe (2009) mapped them. The ecosystems correspond to the "Group" level classification of vegetation types defined in the U.S. National Vegetation Classification (Ecological Society of America et al. 2015). Together the 39 ecosystems cover an area of 1,228,167 km^2. The largest ecosystem is the Western Great Plains Shortgrass Prairie (157,330 km^2), and the smallest is the North American Warm Desert Lower Montane Riparian Woodland and Shrubland (2262 km^2). We

Table 1 Bioclimatic variables and their explanation. Based on Hijmans and others (2005) with the exception of vapor pressure deficit, which is based on Lowry and Lowry (1989) and Snyder and Paw (2002)

Bioclimatic variable	Explanation
Mean annual temperature	The mean of all the monthly mean temperatures
Mean diel temperature range	The mean of monthly diel temperature ranges
Isothermality	The mean diel range divided by the annual temperature range (×100)
Temperature seasonality	The standard deviation of monthly mean temperatures expressed as a percentage of the annual mean (×100)
Maximum temperature of warmest month	The highest temperature of any monthly maximum temperature
Minimum temperature of coldest month	The lowest temperature of any monthly minimum temperature
Temperature annual range	Maximum temperature of warmest month–minimum temperature of coldest month
Mean temperature of wettest quarter	The mean temperature of wettest quarter[a] of the year[b]
Mean temperature of driest quarter	The mean temperature of the driest quarter of the year
Mean temperature of warmest quarter	The mean temperature of the warmest quarter of the year
Mean temperature of coldest quarter	The mean temperature of the coldest quarter of the year
Annual precipitation	The sum of monthly precipitation across the year
Precipitation of wettest month	The total precipitation of the wettest month
Precipitation of driest month	The total precipitation of the driest month
Precipitation seasonality	The standard deviation of monthly precipitation expressed as a percentage of the annual mean
Precipitation of wettest quarter	The total precipitation of the wettest quarter of the year
Precipitation of driest quarter	The total precipitation of the driest quarter of the year
Precipitation of warmest quarter	The total precipitation of the warmest quarter of the year
Precipitation of coldest quarter	The total precipitation of the coldest quarter of the year
Vapor pressure deficit, average annual	The difference between average annual saturation vapor pressure and actual vapor pressure

[a] Quarters are to the nearest month

[b] Years are calendar years

selected this study area because of its sensitivity to habitat alterations from climate change (Seager et al. 2007).

Data types, sources, and preparation

Data used in this study consisted of field plot observations of plant species composition, bioclimatic variables and mapped ecosystem distributions. For the field plots, we used data generated by the USGS National Gap Analysis Program (Prior-Magee et al. 2007) gathered between 2000 and 2003. These data consist of plant species names, percent cover by species, date of observation, geographic coordinates, and ecosystem type in 10 × 10 or 20 × 20 m field plots. We standardized the plant species names to a single synonym using the USDA PLANTS database (USDA Natural Resources Conservation Service 2010) at the species level (subspecies and varieties were dropped).

Spatial data for 19 of the 20 bioclimatic variables was provided by Hijmans and others (2005). These data represent average (i.e., normal) climate conditions between 1950 and 2000. The data occur at a 30 arc-second horizontal cell size at the ground surface, or about 1 km^2 at a spheroid projection. We also included vapor pressure deficit (VPD) as a bioclimatic variable since an elevated VPD increases evapotranspiration, raising environmental aridity and plant desiccation (Lowry and Lowry 1989). Vapor pressure

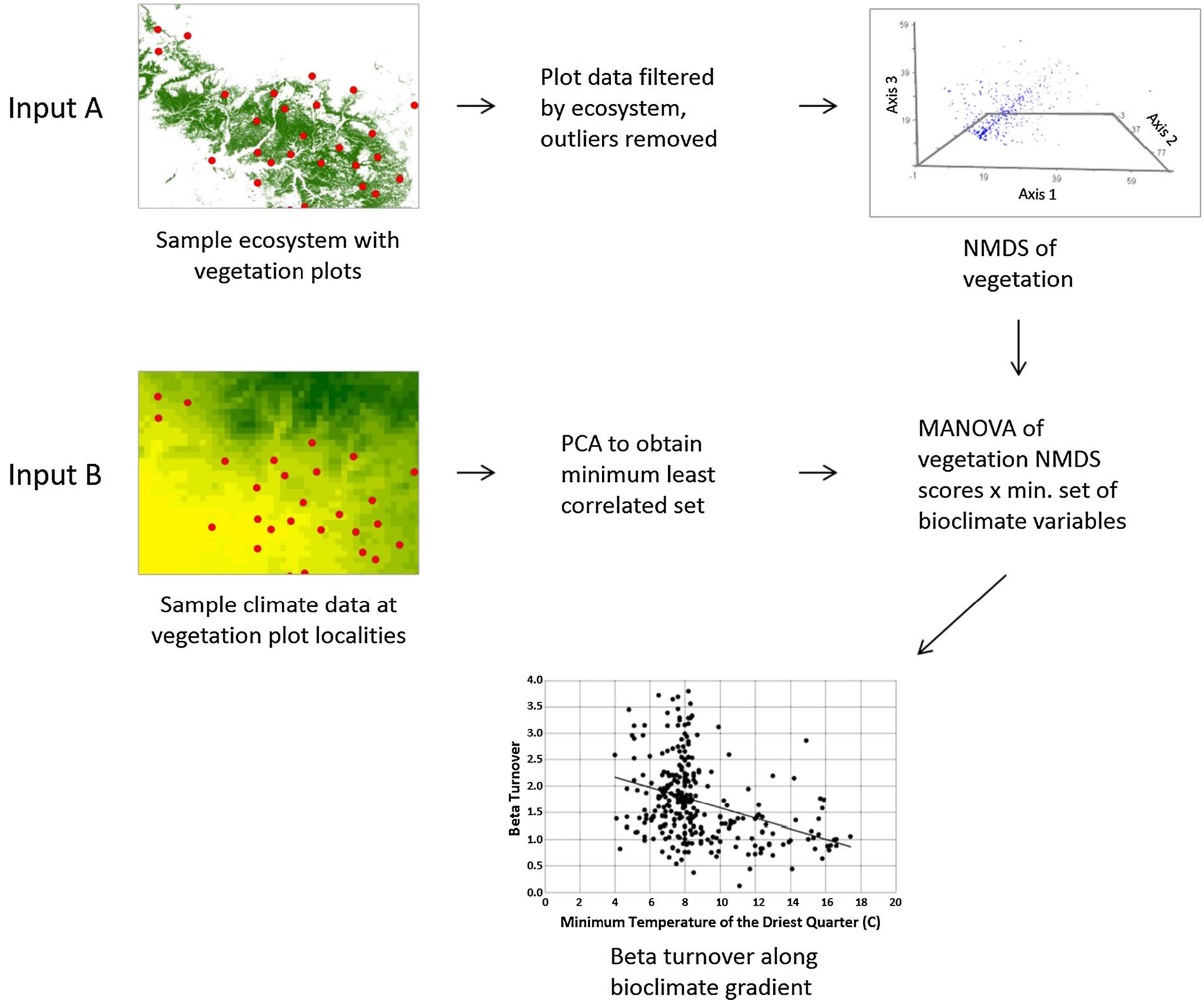

Fig. 2 Analytical process steps. *Input A* shows the steps used to derive the dependent variables (vegetation species composition) while *Input B* shows the steps used to develop the independent variables (bioclimate)

deficit was calculated according to the methods of Snyder and Paw (2002) from data provided by Thornton et al. (2012) spanning 1980–2003. These data occur at a 1 km^2 horizontal cell size at the ground surface.

We relied on GIS data from Prior-Magee et al. (2007) and NatureServe (2009) for geographical occurrences of the 39 ecosystems. These data have a 30 m horizontal ground resolution. Climate variables at each field plot location were extracted from gridded bioclimate datasets of Hijmans et al. (2005) as well as the VPD data derived from Thornton et al. (2012).

In the evaluation of the future amount of ecosystem area projected to retain the same range of bioclimate values as the contemporary climate, projected climate data for the 2030s, 2050s, and 2070s were derived from the GDFL CM3 model (Donner et al. 2011) RCP 8.5 (Moss et al. 2010) downscaled to a 30 arc-second horizontal resolution (Ramirez and Jarvis 2008).

Treatment of vegetation field plot data

The field plot records were stratified by ecosystem and overlaid onto the ecosystem maps. Plots falling outside the boundary of a mapped ecosystem that they had been assigned to during field collection were removed from the analysis. Plots having out-of-range species cover values (>100 % or <1 %) were also removed. For each ecosystem, a matrix of the percent cover for each species in each plot was assembled. A multivariate outlier analysis was performed on these matrices by calculating a Sørenson distance measure of species and their relative abundance (as percent cover) by plot (McCune et al. 2002). Plot records with >2 standard deviations from the mean distance were excluded. Out of an initial 30,380 field plots, 18,533 (61 %) were ultimately used. The number of usable plots per ecosystem ranged from 22 to >2000, with a mean of 475 per ecosystem.

To quantify vegetation composition, the remaining field plot records of each ecosystem were input into a nonmetric multidimensional scaling (NMDS) ordination (Kruskal 1964) using a Sørenson distance measure, a random starting configuration, and a Monte Carlo test. Stress values obtained from the actual data and the Monte Carlo test were compared to evaluate the stability of the final solution. The orthogonality among the output axes was compared to establish the extent to which each represents an independent index of the compositional similarity in species identity and population abundance among the field plots (Appendix 1 in supplementary material).

The NMDS procedure locates each field plot in multidimensional species space, given its coordinate value along each of the axes. Among the axes, the coordinate values indicate the distance and direction of vegetation composition in one field plot relative to all other field plots (McCune et al. 2002). We used the field plot values from three axes as the dependent variables for evaluating the relationships between vegetation composition and the bioclimatic variables within each ecosystem.

Treatment of bioclimate data

Bioclimate values were extracted at each field plot location. Within each ecosystem, values of the 20 bioclimatic variables (Table 1) from the field plot localities were examined for skewness and found to be within normally distributed bounds, though peakedness was evident in some cases. Pearson's correlation coefficients (Pearson 1896) were calculated for each pair of values for the 20 bioclimatic variables per ecosystem. Many of the variables were correlated to some extent. Therefore, we identified a minimum, least correlated set of climate variables that captured ~90 % of the overall climate information present among the field plot localities within each ecosystem. To do this, a principal components procedure (Mardia et al. 1979) was used to reduce the climatic variables to sets of "principal components" ranked by the amount of information retained in each set. Within each principal component, "loading" values describe the relative importance of each variable with respect to the total amount of information represented by each component. Through a process of elimination, variables were identified in each of the highest-ranking components which had both the highest loading values and which were the least correlated with the other variables (that is, the least correlated highest-ranking variables within the top components that explain >90 % of variability). This procedure resulted in a minimum least correlated set of independent, explanatory variables (often four to eight).

Analysis of variance

Each ecosystem was modeled separately. A multivariate analysis of variance (MANOVA) (Grimm and Yarnold 1995) was used to quantify relationships between the NMDS compositional indices of the vegetation plot data and the minimum least correlated set of bioclimatic variables. Bioclimatic variables with a resulting p value >0.05 were rejected. The remaining variables were ranked according to the multivariate Wilks' lambda (λ) and the approximate F-statistic (Bray and Maxwell 1985). Wilks lambda values were transformed to $1 - \lambda$ to indicate the amount of compositional variability explained. The bioclimatic variables with the most explanatory power were those having the highest $1 - \lambda$ in combination with a significant break in the sequence of approximate F-statistic values. In those cases where multiple variables qualified under this procedure, we examined pairwise correlation values between the variables. For those variables with correlations >0.5, the variable having the higher $1 - \lambda$ value was selected. Where more than one bioclimatic variable was identified and correlations were <0.5, the set was retained.

Beta turnover across bioclimate gradients

An informative way to characterize biotic response(s) to an environmental gradient is by the pattern of species turnover along the gradient. This turnover is one form of beta diversity (Whittaker 1972) or beta turnover (Tuomisto 2010). In this application, we expected the change of vegetation along the identified bioclimate gradient to reveal a compositional response to the bioclimatic variable(s). This approach links the magnitude and direction of the compositional changes in vegetation to the corresponding bioclimatic variables, whether the gradients occur across geographical space or time.

The amount of beta turnover was derived using the methods of Oksanen and Tonteri (1995). The fit of beta turnover to bioclimatic variable(s) was described using ordinary least squares regression (Anderson 2008), resulting in the descriptive statistics of: the mean and range of y (beta turnover) values, slope of the fitted line, y intercept, range of y values along the slope, and relative slope. Relative slope is $y_s/y_r \times 100$, where y_s is the range of y values along the fitted slope and y_r is the total range of y values (Appendix 2 in supplementary material). Relative slope was calculated for comparative purposes since the bioclimatic variable units are heterogeneous (e.g., precipitation in mm, temperature in degrees C, and indices such as isothermality) so that the absolute slope values by themselves are not comparable across bioclimate types. The magnitude of the relative slope response in each ecosystem was categorized as strong, moderate, or weak by applying Jenks (1967) breaks to the relative slope vector (Table 2).

Assumptions and limitations

These methods assume that the vegetation composition of the ecosystems respond to particular climate variables, and that these 20 bioclimatic variables adequately explain most of the vegetation composition response to climate in general. Additionally, it is assumed that the relatively large numbers of field observations per ecosystem adequately represent the vegetation heterogeneity of the ecosystems studied. Furthermore, we accepted that: (a) The NMDS procedure adequately represents the multidimensional similarity between any given field plot and all other field plots within a given ecosystem. (b) The PCA procedure robustly identifies the minimum least correlated set of bioclimatic variables that explain about 90 % of the climate information contained in the set of 20 bioclimatic variables. (c) The MANOVA test identifies the minimum set of bioclimatic variables which explain most of the vegetation composition that can be explained by climate; and (d) the method for quantifying a beta turnover gradient is robust.

Limitations to our approach include: (a) Other biophysical processes may also exert control over the composition of the vegetation, making discovery of the climate signal difficult or impossible. (b) Interaction among and rates of change in bioclimatic variables shaping an ecosystem's vegetation composition may consist of more fine grained complexity than our methods are capable of capturing. (c) The methods used here apply to the range of variation within a given ecosystem and do not address invasions of exotic species or altered disturbance regimes.

Results

The vegetation composition in each of the 39 ecosystems responds to distinct bioclimatic variables (Appendix 3 in supplementary material), though the magnitude of response varies. Four of the 20 climate variables explain most of the variability in vegetation composition among the ecosystems. These are: (a) the seasonality of precipitation, (b) the seasonality of temperature, (c) mean annual precipitation and (d) the amount of precipitation during the warmest quarter. These variables form the primary climatic predictors of vegetation composition in 16 ecosystems and contribute to the predictions in 6 others. They explain most of the climate related vegetation composition

Table 2 Number and percent of ecosystems responding to bioclimatic variables by relative slope category. Category thresholds are per Jenks (1967) natural breaks

Beta response category	Number of ecosystems	Percent of ecosystems (%)	Relative slope thresholds
Strong	12	31	>40
Moderate	9	23	27–40
Weak	15	38	<27
Mixed	3	8	

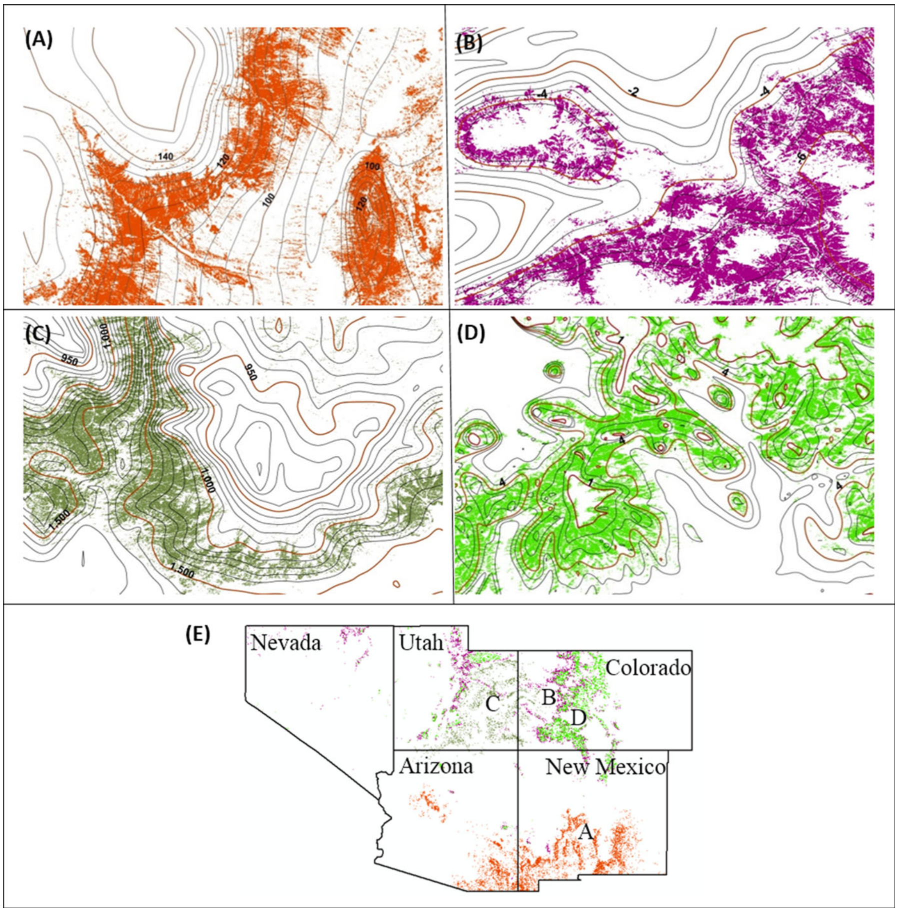

Fig. 3 Landscape scale bioclimate gradients: **a** Contours of precipitation of the wettest month in relation to the Apacherian-Chihuahuan Semi-Desert Grassland and Steppe ecosystem, in *orange*. Contours interval is 4 mm precipitation, scale is 1:250,000. **b** Contours of minimum temperatures of the coldest month in relation to the Rocky Mountain Aspen Forest and Woodland ecosystem, in *purple*. Contours interval is 1 °C, scale is 1:250,000. **c** Contours of precipitation seasonality in relation to the Colorado Plateau Pinyon-Juniper Shrubland ecosystem, in *dark green*. Contours interval is 10 seasonality index points (see definition, Table 1), scale is 1:350,000. **d** Contours of mean temperature of driest quarter in relation to the Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland ecosystem, in *light green*. Contours are at intervals of 1 °C, scale is 1:300,000. **e** Locations of panels (**a**–**d**). Contours derived from data of Hijmans et al. (2005); ecosystem distributions derived from data of NatureServe (2009)

across 752,030 km^2 (61 %) of natural vegetation land cover across the Southwest study area.

Among the 39 ecosystems, beta turnover varied by 95 %. This variability is likely due to the climate niche widths of the prevalent species and the influence of other biophysical factors, such as disturbance, competition, herbivory, and soils. Bioclimate related beta turnover was normalized among the different ecosystems for comparative purposes. A steeper response slope indicates a stronger bioclimate-composition relationship in one ecosystem relative to another. The composition of 12 ecosystems have relatively strong responses to climate, 9 have moderate responses, and 15 significant but relatively weak responses. Three ecosystems showed mixed responses (Table 2).

The Sonora-Mojave Creosotebush-White Bursage Desert Scrub ecosystem had the steepest relative slope (94; Appendix 2 in supplementary material), where beta turnover increased with temperature seasonality. The Rocky Mountain Cliff, Canyon and Massive Bedrock ecosystem and the Rocky Mountain Lower Montane-Foothill Riparian Woodland and Shrubland ecosystem also had steep relative slopes (73 and 66;

Appendix 2 in supplementary material). These ecosystems have strong relationships with precipitation during the driest and coldest quarters, respectively. For both, beta turnover declines with increasing precipitation. Since these three ecosystems have large beta turnover, they hold a high potential for changes in vegetation composition across geographical space relative to changes in the bioclimatic variables predicting them.

The geographical areas within ecosystems where the bioclimate gradients are steeper are more likely to experience greater changes in vegetation composition over space and time. To identify and describe places where such gradients occur, spatial contours of the explanatory bioclimatic variables were overlaid onto maps of the ecosystem's distributions. Ecosystems having a strong to moderate relationship with bioclimate show considerable spatial correspondence between the ecosystems' landscape configuration and bioclimate contours (Fig. 3).

With the composition-bioclimate approach, floristically based climatic boundaries of ecosystems can be identified, which better resolves ecosystem types. For example, vegetation of the Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland ecosystem is best explained by the minimum temperatures during the driest quarter. Yet this relationship is not uniform. One area of this ecosystem has a relative beta diversity response slope 3.6 times greater than the other, whereby beta turnover increases as temperature drops (Appendix 4 in supplementary material). Although mapped and described as a single ecosystem (NatureServe 2009), the methods used here capture a distinct separation (see Sesnie et al. 2012).

We linked 11 southwestern ecosystems having strong bioclimatic relationships with downscaled projections of future climates (Ramirez and Jarvis 2008; Donner et al. 2011). This step illustrates how a better understanding of the relationships between bioclimate and ecosystem vegetation composition can address applied problems. The resulting estimates describe how ecosystem vegetation might change in future decades (2030s, 2050s, 2070s), given reconfigurations of the bioclimate variables required by an ecosystem's current vegetation. In doing so, these results identify where changes in ecosystem vegetation may occur and their pace (Appendix 5 in supplementary material).

Projections of future climates indicate that 7 of the 12 ecosystems with strong bioclimatic responses are expected to experience large changes to their area of suitable climate (Appendix 5 in supplementary material). For example, by the 2070s, the Sonora-Mojave Creosotebush-White Bursage Desert Scrub ecosystem is forecast to lose ~15 % of its bioclimatic area. The extent of this ecosystem is large (46,000 km^2) and the percent of loss equates to ~7000 km^2, roughly the size of the U.S. state of Connecticut. The Western Great Plains Sandhill Steppe is also relatively large and the amount of bioclimate area lost (31 %) equates to ~4000 km^2—an area 1.3 times the size of Rhode Island.

The North American Warm Desert Lower Montane Riparian Woodland and Shrubland ecosystem is relatively small (~2000 km^2). However, by the 2070s, half of its bioclimatic area is projected to consist of a different climate, and likely a different ecosystem type (Appendix 5 in supplementary material). Importantly, riparian ecosystems are keystone habitats, hubs of biological diversity and essential for sustaining life processes in arid landscapes (Chambers and Miller 2004). Given the amounts of change in vegetation composition that is possible over a short period (~50 years), the consequences for biodiversity and its stewardship in riparian along with surrounding ecosystems could be substantial.

Results also show how alterations to an ecosystems' vegetation composition can occur internally, even when the climatic conditions that best explain its composition remain within the overall range of contemporary values but change geographically. For example, the Madrean Pinyon-Juniper Woodland ecosystem has a strong relationship with precipitation seasonality (relative slope = 42; Appendix 2 in supplementary material). Presently, the distribution of values for precipitation seasonality span 43–132 units. By the 2030 s the overall range of these values is reduced by one-half, yet this reduced range of values still occupies the contemporary geographic distribution of the ecosystem (Fig. 4). Although the total ecosystem area is expected to remain unchanged through the 2070s, the range of climatic variability across this 18,927 km^2 landscape narrows markedly. Its vegetation composition is expected to become more uniform. The implications for this ecosystem, whether increased vulnerability to disturbances, a reduction in habitats for vertebrates, or altered provisioning of ecosystems services, remain unknown.

Discussion

Although other biophysical dynamics influence species composition to a greater or lesser degree, the approach taken in this study isolates the influence of climate on vegetation composition. The stepwise process enables testing, calibration, and evaluation throughout each interval of the modeling sequence.

Our methods revealed a striking relationship between the Madrean Pinyon-Juniper Woodland ecosystem and precipitation seasonality (i.e. the range of variability in the seasonality of precipitation). This relationship demonstrates three facets of ecosystem change (Fig. 4). Namely: (a) The magnitude of the change in the variability of the seasonality metric itself; (b) That the change is not uniform across the ecosystem's geographic occurrence. Instead, the change exhibits a strong spatial dependency. (c) The change in the variability of this ecosystem's primary bioclimatic variable occurs within the ecosystem's current climate space. Hence, the spatial distribution of the ecosystem's overall climate envelope remains unchanged, yet internally the variability of seasonal precipitation changes dramatically. In aggregate, this example shows how changes in an ecosystem's suitable climate can be more nuanced than simple shifts in presence-absence. We anticipate that further analyses will reveal other critical but complex

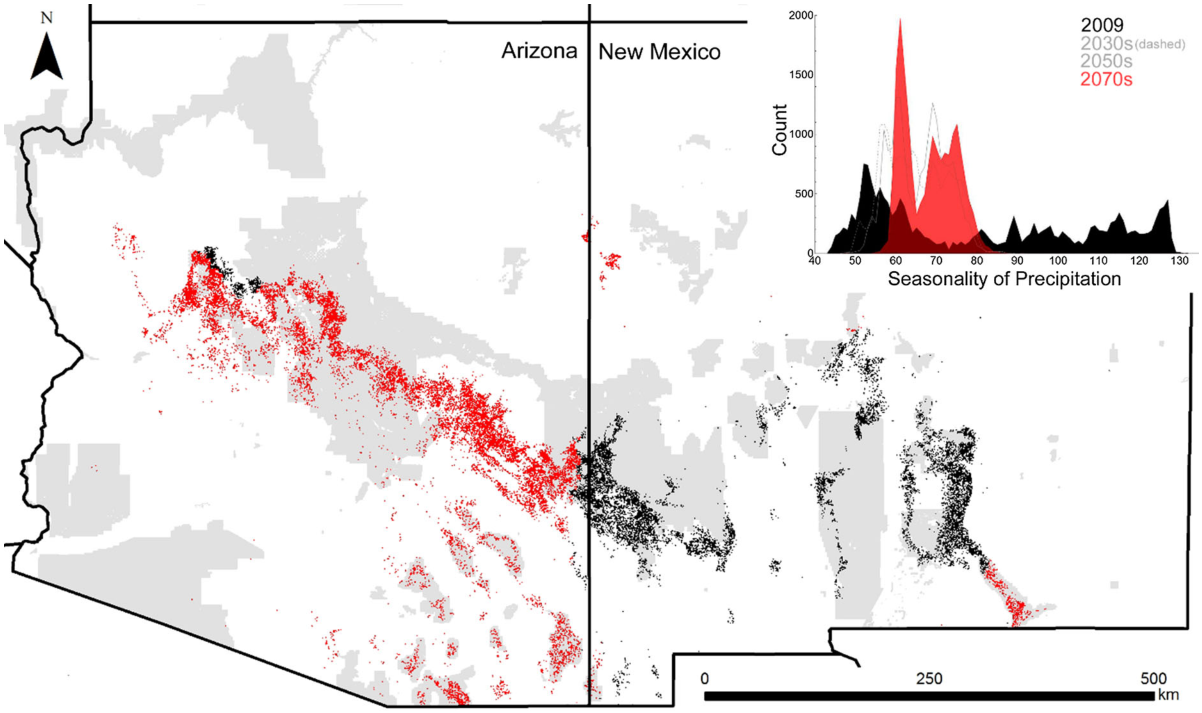

Fig. 4 Geographical distribution of the Madrean Pinyon-Juniper Woodland in the southwestern United States (states of Arizona and New Mexico). This ecosystem has a strong relationship with the seasonality of precipitation (i.e. annual variability of precipitation; Appendix 2 in supplementary material). The location of *red* and *black* pixels illustrate the geographical distribution of this ecosystem's bioclimate, which remains unchanged from 2009 to 2070s. *Red pixels* identify seasonality of precipitation values of 47–91, while *black* indicates all other values. In 2009, pixel values range from 43 to 132, as depicted in the figure (*red* and *black pixels*, depending on their value). By the 2070s, the range of seasonality of precipitation values are halved to 47–91 (*red colored pixels*), mainly from a contraction in the higher values. Therefore, all of the pixels in the figure are predicted to remain this ecosystem type in the 2070s (but given their values, they would be colored *red* in the figure). The effects of reduced precipitation variability across this ecosystem's geographical space, regarding its resilience to disturbance or other dynamics is unknown. *Gray polygons* identify property administered by the U.S. Department of Defense, U.S. Fish and Wildlife Service, U.S. Forest Service and the National Park Service. Count represents pixels of 1 km^2

expressions of altered bioclimates. Such knowledge should lead to a far greater understanding of how climate change influences large ecosystems. Societal responses to climate induced changes in ecosystem services could become more successful as a result.

The Madrean Pinyon-Juniper Woodland ecosystem exhibited a large change in precipitation seasonality between the reference period and the 2030s, as well as between the 2030s and the 2070s. As above, these changes are strongly geographic. They correspond to land form in combination with their position relative to the Gulf of Mexico. We speculate that this spatial change in the variability of precipitation seasonality is related to future changes in the monsoonal dynamics of the region.

To exemplify the application of our methods to future climates, we relied on the RCP 8.5 climate scenario from the GFDL CM3 model. Our rationale for using a single model, and the GFDL CM3 in particular, is that of the many factors to consider when deciding on appropriate climate data inputs for modeling, one must first identify the object of interest. In this case, the object is biotic responses to climate (as opposed to, for example, the response of ocean circulation or cryosphere dynamics to climate). Biota do not respond to climate per se, but to particular climatic conditions that limit or facilitate their establishment or persistence (i.e. bioclimatic variables). Therefore, it is critical that the climate data used expresses such limitation or facilitation thresholds well. However, these characteristics often occur as extremes located in the tails of the distribution. While ensemble data serve a useful purpose in expressing the central tendency among a suite of general circulation models, the signals that limit or facilitate biotic occurrence may be dampened or otherwise skewed (e.g., Vavrus et al. 2015) by an ensemble's rules of combination. As discussed by Tebaldi and Knutti (2007), the reliance on consensus estimates via ensembles carry inherent challenges, including (a) the choice of metrics and diagnostics of performance, (b) inter-model dependencies and common biases, (c) compounding of errors, and (d) the representativeness of the sample of models with regard to common fundamental uncertainties. This is not to say that the central tendency in the suite of models is unimportant. Instead, our point is that because of these issues, we chose a single, well-vetted model performing close to the ensemble central tendency to derive future projections of bioclimatic variables. A full analysis describing projections of future vegetation composition via multiple climatic scenarios is beyond the scope of this paper. This topic is, however, being addressed in ongoing work.

By swapping space for time (Ferrier and Guisan 2006; Elith and Leathwick 2009) along the climate-composition gradient, a first order explanation of how vegetation composition is likely to change in response to incremental changes in primary climate variables is possible. Blois et al. (2013), caution that at time scales of years or spatial resolutions of kilometers or less, stochastic processes could limit the utility of space-for-time substitution. However, the landscapes in this study cover areas of hundreds to many thousands of square kilometers, and are currently experiencing extraordinarily rapid climate change. Therefore, we expect this approach to be useful for anticipating changes of habitat composition over time across large landscapes and at the resolution of conservation and management areas. The methods in this study can also provide a reference framework for addressing the quandary over managing for the historical compliment of species in an area versus a changing composition of species and the direction such changes may take.

Our methods are applicable to a wide range of other problems. For example, recently the technical criteria for assessing threats to the persistence of ecosystems under the IUCN's Red List of Ecosystems (RLE) (Rodriguez et al. 2011; Keith et al. 2013) was questioned for its adequacy in the face of climate change (Boitani et al. 2015). Boitani et al. (2015) argue that the current RLE approach is inadequate because it lacks criteria for determining where along the compositional continuum of space and time an ecosystem ceases to exist. The methods for quantifying the relationships between ecosystem composition and gradients of environmental forcings provide the criteria for improving the RLE by delineating the bioclimatic boundaries of terrestrial ecosystems. Additionally, these methods provide a mechanism for quantifying the sensitivity of vegetation composition to the magnitude and rate of climate change, thereby aiding ecosystem threat assessment.

Conclusion

Results from this study reveal several dimensions of how climate change influences the composition of terrestrial ecosystems. The methods provide the specific climate and vegetation parameters required for anticipating how, where and when ecosystem vegetation transforms with climate change. This information enables a ranking of ecosystems by their sensitivity to altered climates, thereby increasing the efficacy of resilience planning. Assessing ecosystem threats and predicting the future vegetation composition of ecosystems grows ever more important given the amount of climatic flux the planet is experiencing and the rates of changes expected (IPCC 2014).

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