



Multiple axes of ecological vulnerability to climate change

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Funding information

National Science Foundation, Grant/Award Number: GRFP; U.S. Bureau of Land Management

Abstract

Observed ecological responses to climate change are highly individualistic across species and locations, and understanding the drivers of this variability is essential for management and conservation efforts. While it is clear that differences in exposure, sensitivity, and adaptive capacity all contribute to heterogeneity in climate change vulnerability, predicting these features at macroecological scales remains a critical challenge. We explore multiple drivers of heterogeneous vulnerability across the distributions of 96 vegetation types of the ecologically diverse western US, using data on observed climate trends from 1948 to 2014 to highlight emerging patterns of change. We ask three novel questions about factors potentially shaping vulnerability across the region: (a) How does sensitivity to different climate variables vary geographically and across vegetation classes? (b) How do multivariate climate exposure patterns interact with these sensitivities to shape vulnerability patterns? (c) How different are these vulnerability patterns according to three widely implemented vulnerability paradigms—niche novelty (decline in modeled suitability), temporal novelty (standardized anomaly), and spatial novelty (inbound climate velocity)—each of which uses a distinct frame of reference to quantify climate departure? We propose that considering these three novelty paradigms in combination could help improve our understanding and prediction of heterogeneous climate change responses, and we discuss the distinct climate adaptation strategies connected with different combinations of high and low novelty across the three metrics. Our results reveal a diverse mosaic of climate change vulnerability signatures across the region's plant communities. Each of the above factors contributes strongly to this heterogeneity: climate variable sensitivity exhibits clear patterns across vegetation types, multivariate climate change data reveal highly diverse exposure signatures across locations, and the three novelty paradigms diverge widely in their climate change vulnerability predictions. Together, these results shed light on potential drivers of individualistic climate change responses and may help to inform effective management strategies.

KEYWORDS

biogeography, climate change, climate departure, climate velocity, niche model, novel climate, resource management, vegetation, vulnerability

1 | INTRODUCTION

Biotic responses to climate change are characterized as much by their individuality as by their generality. Contemporary and paleoecological records show that the impacts of changing climate are widespread but highly varied, with novel ecological communities emerging as species range edges expand and contract individually in direction and degree (Jackson & Overpeck, 2000; Nolan et al., 2018; Rapacciolo et al., 2014). These realities present both a puzzle to ecological understanding and a grave challenge to future resource management, which requires scientifically sound vulnerability predictions to guide local and regional climate change adaptation efforts. Improving our understanding of the many factors that underlie this variation is an important priority. Here we use terrestrial vegetation types of the western US as a case study to explore several layers of spatial and ecological variation that underlie emerging patterns of vulnerability to climate change over recent decades.

Climate change vulnerability is defined as the degree of threat to a population, species, or ecosystem in response to changing climate, and differences in vulnerability across systems are often conceived of as resulting from their differing levels of exposure, sensitivity, and adaptive capacity (Dawson, Jackson, House, Prentice, & Mace, 2011). Developed originally to describe climate vulnerability of human systems, this framework has now been widely applied in the ecological realm, though operational definitions and metrics for the three components have been inconsistent across studies. Similarly to prior studies (Dawson et al., 2011), we define exposure as the magnitude of extrinsic change in climate itself, sensitivity as the amount of detrimental change that will result from a given amount of exposure, and adaptive capacity as the intrinsic ability of an individual, population, or ecosystem to naturally reorganize without collapse and maintain function given particular levels of exposure and sensitivity.

While obtaining detailed measurements of these vulnerability components is infeasible at the macroecological scales needed for applications such as regional conservation planning, recent studies have begun to explore how proxies for these components may explain the variability in observed climate change impacts across species. Species-level ecological or phylogenetic traits offer one category of proxies: range shifts have been found in some systems to correlate with sensitivity-related traits such as ecological generalization (e.g., Angert et al., 2011), adaptive capacity-related life history traits connected to growth, reproduction, and dispersal (e.g., Beaver et al., 2016; Lenoir, Gegout, Marquet, Ruffray, & Brisse, 2008; Wolf, Zimmerman, Anderegg, Busby, & Christensen, 2016), and phylogenetic relationships that likely capture covariance among many such traits (e.g., Willis, Ruhfel, Primack, Miller-Rushing, & Davis, 2008). But meta-analyses have repeatedly found that these ecological and taxonomic traits have low explanatory power, accounting for at best a small proportion of the observed variation in recent climate change responses (Buckley & Kingsolver, 2012; MacLean & Beissinger, 2017; Rapacciolo et al., 2014; Wiens, 2016).

Ecological responses have also been shown to correlate with exposure, though most studies have focused on changes in individual

climate variables such as mean annual temperature, which tends to significantly but only weakly predict observed shifts in species distributions (e.g., Rumpf, Hülber, Zimmermann, & Dullinger, 2018). Recent work has noted the likely importance of concurrent but differing changes in multiple climate variables in driving geographic variation in ecological responses (Dobrowski et al., 2013; Hamann, Roberts, Barber, Carroll, & Nielsen, 2015; Nadeau & Fuller, 2015; Rapacciolo et al., 2014). If climate variables exhibit different spatial patterns of change, then biogeographic responses have the potential to be complex, with species shifting in different directions and non-analog communities emerging (Jackson & Overpeck, 2000; Ordonez, Williams, & Svenning, 2016; Tingley, Koo, Moritz, Rush, & Beissinger, 2012). This will be particularly true if species differ in the variables to which they are most sensitive.

Biogeographic patterns of climate sensitivity have, like exposure, been studied primarily in a univariate context focused on temperature. Temperature sensitivity patterns are thought to underlie fundamental biogeographic patterns such as the latitudinal range size gradient (Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006) and predicted to strongly shape patterns of vulnerability to contemporary climate change (Dillon, Wang, & Huey, 2010; Tewksbury, Huey, & Deutsch, 2008). But since climate change exposure clearly encompasses much more than mean temperatures, a broader, multivariate understanding of sensitivity to different aspects of climate is essential to predicting vulnerability. While it is common practice in species distribution modeling to evaluate variable importance, this is typically done on a case-by-case basis. Patterns of multivariate climate variable importance at a macroecological scale have remained largely unexplored. Several recent studies have begun to address this gap (Barbet-Massin & Jetz, 2014; Bradie & Leung, 2017; Schuetz et al., 2019), though few have explored potential trends in variable importance among locations, environments, or biomes. In this study, we quantify patterns of climate variable importance across vegetation types and across spatial and climatic gradients, and assess how these sensitivities intersect with patterns of multivariate climate exposure to shape predicted vulnerability at landscape to regional scales.

Beyond geographic patterns of climate exposure and biotic patterns of sensitivity to those variables, a third consideration is that geographies and biotas may experience different dimensions of climate novelty. The literature is full of indices used to estimate ecological vulnerability from multivariate climate exposure patterns, including climatic niche modeling (Elith & Leathwick, 2009), climate change velocity (Hamann et al., 2015; Loarie et al., 2009), standardized anomalies (Mahony & Cannon, 2018; Williams, Jackson, & Kutzbach, 2007), expanding and contracting climates (Ackerly et al., 2010), and numerous others (Garcia, Cabeza, Rahbek, & Araújo, 2014). We argue that most of these approaches relate to one of three basic vulnerability paradigms—the 'niche', 'temporal', and 'spatial' paradigms—each of which provides one answer to the question of how novel a new climate regime is to the group of organisms living at a given site. (Note that the term 'novel climate' has sometimes been used in narrower reference to spatiotemporal climate novelty metrics [Mahony,

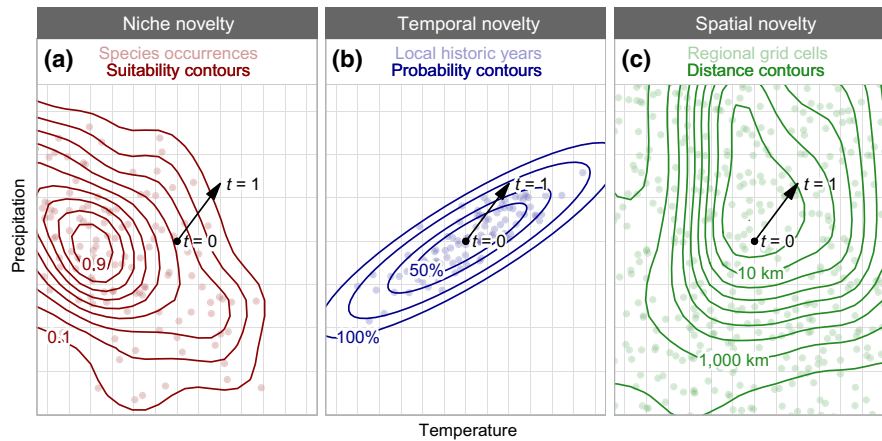


FIGURE 1 Conceptual diagram of the three dimensions of climate novelty explored in this paper, illustrated for a single focal site for two climate variables. The site has a historic mean climate ($t = 0$) that shifts as climate changes ($t = 1$), defining an exposure vector in multivariate climate space (black arrow). While the climate axes and climate exposure vector are identical across the three novelty metrics, each novelty paradigm evaluates this exposure against a different reference probability distribution (colored points). These distributions represent proxies for sensitivity and/or adaptive capacity, and each generates a distinct assessment of climate change vulnerability (contour lines) that increases as climate moves away from the center of the distribution. (a) The niche paradigm uses mean historic climates across all occurrences of a species or vegetation type to define suitability, and measures novelty as the decrease in suitability with climate change. (b) The temporal paradigm defines novelty as the degree of departure from year-to-year historic climate variability at the site, which we quantify as a Mahalanobis distance percentile. (c) The spatial paradigm defines novelty as the geographic distance to locations with historic climates similar to the site's new climate, which we quantify using inbound climate velocity. The three reference distributions, the exposure vector, and the most appropriate climate axes will differ across sites and across focal taxa or ecosystems, yielding different combinations of high and low vulnerability values across the three metrics; each of these drivers of predicted vulnerability patterns is explored in this paper

Cannon, Wang, & Aitken, 2017; Williams et al., 2007], which are not neatly categorized in this framework since they combine two of the three novelty paradigms in a single index.) Each of these three novelty paradigms takes the same climate exposure value (difference in climate between two time periods) and combines it with a different proxy for sensitivity and/or adaptive capacity to generate a distinct estimate of vulnerability (Figure 1), as detailed below. Our terms for the three paradigms refer to these distinct proxies, though all are of course 'temporal' in relating to climate change over time.

The niche novelty paradigm predicts high vulnerability to conditions that are outside the range of long-term average climates across the geographic distribution of a focal species or ecosystem type, employing space-for-time substitution to predict local responses to climate change (Figure 1a). This ecological niche modeling approach has been widely applied both to species (Elith & Leathwick, 2009) and to vegetation types (Ackerly, Cornwell, Weiss, Flint, & Flint, 2015; Comer et al., 2013; Thorne, Boynton, Holguin, Stewart, & Bjorkman, 2016; Thorne et al., 2018). It hinges on the assumption that populations of a 'species' or plant communities of a vegetation 'type' share a niche if they share a name, as well as the assumption that realized climatic niches reflect fundamental climatic niches. These assumptions are often violated by ecological realities such as local adaptation, dispersal limitation, spatially non-stationary biotic interactions, soil specialization, and rare historical climate events that have shaped geographic distributions. Empirical challenges such as limitation and bias in the quantity, accuracy, and scale of spatial biological and environmental data further strain the ability of climate niche models to accurately reflect climate change vulnerability. It is

thus unsurprising that niche models often fail to predict observed biotic responses to climate change—or perhaps more generously, surprising that they succeed as often as they do. Challenging at the species level, niche models present additional problems at the scale of communities like vegetation types whose ecology may be determined less by classical species niche evolution than by the contingent intersections of individual species.

The temporal novelty paradigm instead predicts high vulnerability to conditions that are outside the range of local year-to-year climate variability at the focal site (Figure 1b), a proxy for the known survived experience of local populations (Klausmeyer, Shaw, MacKenzie, & Cameron, 2011; Williams et al., 2007). Temporal novelty assumes that the climatic tolerance of a local biota is connected to local historical temporal variability in climate, with ecological and evolutionary processes in sites with high climate variability selecting for species and genotypes with broader individual or collective tolerances. High temporal variability could select for resilient individuals in long-lived species, and for adaptive genetic variation in populations of short-lived species. Connections between climate variability and tolerance have roots in long-standing macroecological hypotheses such as Janzen's (1967) treatise on high tropical mountain passes and Rapoport's rule about latitudinal gradients in niche breadth (Stevens, 1989), and have gained renewed attention in recent work on climate change vulnerability (Klausmeyer et al., 2011; Li, Wu, Liu, Zhang, & Li, 2018; Mahony & Cannon, 2018; Mora et al., 2013; Sandel et al., 2011; Tewksbury et al., 2008). In cases where it is suspected that local adaptation, extreme climate events, or range limitation by non-climatic factors are important, or where the idea of

an evolutionarily coherent climatic niche seems inappropriate due to the nature of the focal system, local historic variability may provide a better proxy for sensitivity than do range-wide niche models.

Finally, the spatial novelty paradigm predicts high vulnerability to conditions that are outside the range of historic mean climates across locations in the geographic region around the focal site (Figure 1c; Hamann et al., 2015), emphasizing an aspect of vulnerability more connected to adaptive capacity than to sensitivity. The ability of a local population or ecosystem to maintain function through reorganization (i.e., its adaptive capacity) will depend in many systems on the rate of arrival of novel genes or species better suited to the new climate regime, replacing those with declining fitness *in situ* (Beever et al., 2016). This adaptive genetic and community turnover will, in turn, depend on the proximity of source areas with suitable migrants; when climate warms, sites that are close to historically warmer areas will be more likely than sites isolated from warmer areas to receive new genes and species that are evolutionarily adapted to the new climate. A full characterization of propagule availability and adaptive gene flow would be a function of the frequency distributions of climate conditions at increasing distances from a focal site, together with the dispersal capacity of the organisms. This can be approximated with backward climate velocity (Hamann et al., 2015), which measures the distance from a site to the nearest location with a historic climate similar to the site's new climate. Rather than 'backward' and 'forward' velocity, here we use the terms 'inbound' and 'outbound' velocity, which we believe are more intuitive and will facilitate future discussion.

Given their distinct approaches, each of these novelty paradigms potentially has an important place in holistic vulnerability assessments at the macroecological scale, and each approach will have strengths and weaknesses for particular study systems. While each metric will predict higher vulnerability given higher exposure, these vulnerability magnitudes also have the potential to differ substantially. However, it remains largely unexplored how they compare empirically in terms of vulnerability patterns across landscapes and ecosystem types (though see Garcia, Cabeza, Altwegg, & Araújo, 2016 for a study on African vertebrates). If these alternative novelty metrics are positively correlated, as might be expected since all are based on the same strongly patterned climate exposure values, then their conceptual distinctions are unlikely to result in contrasting ecological patterns and they can be considered redundant in conservation applications. But if they diverge in their vulnerability estimates, then it raises important questions about what metrics to consider in which ecological contexts, and about what management strategies to pursue in relation to intersecting measures of climate novelty.

In this study, we address three broad questions about emerging patterns of vulnerability to recent climate change across the distributions of 96 vegetation types covering more than two million square kilometers of relatively intact landscapes in the western US. (a) How does sensitivity to different climate variables, measured as predictive importance in distribution models, vary across vegetation types and geographic gradients? (b) How do these sensitivity patterns interact with multivariate climate change exposure patterns to

shape predicted vulnerability across ecosystems in the region? (c) How correlated are niche, temporal, and spatial novelty dimensions, and what are the management implications for ecosystems considered to have different combinations of high and low vulnerability on these three axes?

2 | METHODS

2.1 | Study area

Our study focused on terrestrial vegetation of the conterminous US west of 95°W longitude, an area selected for having high-quality data on vegetation and climate, a high degree of ecological diversity, and relatively high intactness of native vegetation. This region encompasses hot and cold desert shrublands, diverse grassland habitats, and forests ranging from coastal temperate rainforest to oak savannah to subalpine coniferous forest, as well as various important alpine, lowland, and substrate-driven sparsely vegetated types.

2.2 | Vegetation data

Our analysis is based on the NatureServe Terrestrial Ecological Systems, a classification of 642 vegetation 'types' that have been extensively described and mapped at high resolution by resource managers in the conterminous US through a combination of remote sensing and extensive ground surveys (Comer et al., 2003; Gergely & McKerrow, 2016; Rollins, 2009) and widely used in ecological assessments (e.g., Aycrigg et al., 2013; Comer et al., 2013, 2019; Thorne et al., 2018). Each of these vegetation types represents a recurring natural plant community defined by dominant and diagnostic plant species and their characteristic environment (Comer et al., 2003). Each type also equates to a Group or Alliance within the hierarchically structured US National Vegetation Classification (USNVC; Faber-Langendoen et al., 2014), and types can thus be aggregated to broader classification levels (Macrogroup, Division, Formation, Subclass, Class).

We used existing data on the distributions of each type across the conterminous US from the LANDFIRE dataset (Rollins, 2009) as well as corresponding data from Canada and Mexico (P. Comer, unpublished data) which are based on hundreds of thousands of georeferenced ground-based vegetation samples in combination with satellite imagery, climate, and landform data. These 90 m resolution gridded spatial data include both existing vegetation type (EVT) maps representing contemporary distributions and biophysical setting (BPS) maps representing the estimated pre-Columbian extent of each type (Rollins, 2009).

To select types for analysis, we first eliminated anthropogenic cover types and vegetation types with less than 50% of their range falling within the western US study area. Next, we ranked types in descending order of land area within the study area, and selected

the first n types that cumulatively covered 90% of natural land area. Several riparian and wetland vegetation types were removed to limit the analysis to upland vegetation deemed likely to be climate-limited. This resulted in a final set of $n = 96$ vegetation types (Figure S1) that collectively represent the vast majority of natural lands in the western US.

To match the scale of the climate data described below, the 90 m resolution grid of each vegetation type distribution was converted to a coarser 810 m resolution grid, with values representing the fraction of 90 m cells occupied by a type. This was done for both the EVT and BPS datasets.

2.3 | Climate data

Gridded historic climate data interpolated from weather station measurements were obtained from TopoWx (Oyler, Ballantyne, Jencso, Sweet, & Running, 2014), PRISM (Daly et al., 2008), and ClimateNA (Wang, Hamann, Spittlehouse, & Murdock, 2012). TopoWx was considered most robust due to its use of remote sensing data and algorithms to correct weather station inhomogeneities that can confound climate trends, but it only includes temperature variables and is limited to the United States. We supplemented this with monthly precipitation data from PRISM, which uses the same spatial grid and extent and a nearly identical set of input weather station data as TopoWx. Data for Canada and Mexico, which are outside our study area and used only for a small portion of the analysis, were obtained from ClimateNA. These datasets all comprise four monthly climate variables (average daily mean temperature, average daily maximum temperature, average nightly minimum temperature, and total precipitation) for each month of each year from 1948 to 2014.

For each year in these time series, we derived 19 bioclimatic variables (Table S1) from the 48 monthly variables following the methods of O'Donnell and Ignizio (2012). We then calculated multidecadal means of these bioclimatic variables for baseline (1948–1980) and recent (1981–2014) periods. 1980 was chosen as a breakpoint since global temperatures were already trending steadily upward in the 1980s (IPCC, 2014) and we wanted to avoid these trends biasing estimates of baseline climates.

2.4 | Climate variable sensitivity

To evaluate the relative importance of the 19 climate variables for each of the 96 vegetation types, we trained niche models using different combinations of climate variables, and tested their performance in predicting the distributions of each vegetation type. Niche models were fit using BPS data to avoid bias from human land use change, and were fit based on the entire Mexico–US–Canada range of each type, including areas outside the main study area. Models were trained within the rectangular bounding box encompassing each type, to emphasize climate gradients that

differentiate neighboring vegetation types at landscape scales. They were fit using presence–absence as the dependent variable, with presence defined as one or more 90 m occurrences within an 810 m grid cell.

Our model testing framework used recursive feature elimination (RFE) to rank the climate variables for each type, based on a combination of spatial block cross-validation (SBCV) and pairwise distance sampling (PWDS) used to evaluate model performance in the presence of spatial autocorrelation. We performed this process for each of five niche modeling algorithms (GAM, GLM, Mahalanobis distance [MD], MaxEnt; Phillips & Dudík, 2008, and random forest), including multiple specifications and tuning parameter values for each algorithm. The random forest classification algorithm performed best on average across vegetation types, and was used in the final analysis (with parameters $n_{tree} = 10,000$, $nodesize = 8$, and $mtry = 1$ tuned to optimize performance). The final variable importance analysis using the random forest algorithm involved fitting and evaluating a total of 2,903,040 separate niche models: 96 vegetation types \times 189 RFE variable sets \times 8 SBCV folds \times 20 randomized repetitions per fold.

Recursive feature elimination variable selection for each vegetation type begins with all 19 variables, tests the predictive performance of 19 sub-models each with a single variable removed, and then eliminates the variable that least negatively impacted predictive performance. It then repeats this process for the remaining 18 variables, and so on until only one variable remains, deriving a ranking of variable importance based on elimination order. Uninformative variables removed at each step may be ecologically unimportant and/or may be statistically redundant with other variables due to high correlations.

For each vegetation type, this RFE process involves hundreds of evaluations of model performance. When testing predictive performance, it is critical to test models on data that are independent from the training data used to fit them. Because both climate and the ranges of vegetation types are spatially autocorrelated, randomly selected training and testing points will be non-independent. We thus used SBCV to measure performance in predicting to a spatially separate domain (Bahn & McGill, 2013), by dividing the range of each vegetation type into four north–south strips each containing 25% of presence localities, and iteratively using three of these blocks for training and one for testing, and then repeating the process using four east–west strips. For each of these eight ‘folds’, we selected testing presence and absence points using PWDS (Hijmans, 2012) to further control the bias from spatial autocorrelation near the boundaries of spatial blocks, and measured predictive performance using the area under the receiver-operator curve (AUC) statistic. For each fold, 20 randomized models was fit, each using a random sample of 1,000 presences and 1,000 absences. Mean AUC across the eight folds and 20 randomizations were used to identify the least informative variable at each step of the RFE progression.

This analysis generated variable importance rankings for each of the 96 vegetation types (Figure S2), which we used in two ways.

First, for each type, we selected the four most important variables for use in the niche, temporal, and spatial novelty analyses as detailed below. The choice to use four variables was based on observed model performance during RFE—mean AUC began declining rapidly with fewer than four variables but barely improved with more than four, making this a reasonable tradeoff between parsimony and information content (Figure S3). Second, we used these data to quantify similarity among vegetation types in the variables most important in shaping their distributions, by performing a principal component analysis (PCA) ordination of the 19×96 matrix of variable importance values; in this analysis, a climate variable that for example loads positively onto PC1 will tend to have relatively high importance for the vegetation types with positive PC1 values, and relatively low importance for types with negative PC1 values.

2.5 | Niche novelty

To calculate niche-based vulnerability, we quantified departure from the realized range-wide climate niche of a vegetation type. For each vegetation type, a final random forest niche model was fit as described above, using the full distribution of the type and using the baseline mean climate data for the four most important variables for that type. Models were then used to predict suitability across the existing (EVT) distribution of each vegetation type for both the baseline and recent time periods. Niche novelty in each cell was calculated as recent minus baseline suitability, with all negative values coded as zero. Positive values thus represent declining suitability (with a maximum possible value of one), whereas zero values represent stable or increasing suitability.

2.6 | Temporal novelty

We used standardized anomalies (Mahony & Cannon, 2018) to calculate the degree of climatic departure from local baseline year-to-year variability. Specifically, we calculated the MD of the recent mean with respect to the baseline time series. Separately for each grid cell occupied by each vegetation type, the four variables most important to the type were reduced to their first two principal components based on a PCA of their local temporal covariance structure, and then the MD of the recent mean was calculated relative to these principal components. This dimension reduction was done to avoid overemphasizing the biological significance of high-dimensional climatic covariance. We report these MD values as percentiles for communication purposes, by computing MD for each individual year in the baseline and calculating the fraction of baseline years whose MD value is exceeded by the recent mean; these percentile values work well for the moderate recent trends assessed here but would saturate with continued future climate change. MD values and percentiles are most interpretable when data are relatively multivariate normal, which we confirm is indeed the case for our analysis (Figure S4).

2.7 | Spatial novelty

To calculate vulnerability defined by climates being new to the geographic neighborhood around each grid cell, we calculated multivariate inbound (backward) climate velocity (Hamann et al., 2015) for each grid cell occupied by each vegetation type. The four variables most important to a given type were de-skewed using a Yeo-Johnson power transformation to produce a relatively normal distribution across the continent. Following closely the methods of Hamann et al. (2015), we converted the climate data to a Lambert conformal conic projection, used a PCA to reduce the dataset to two dimensions, split each dimension into 100 equal-interval bins, and finally calculated multivariate inbound climate velocity. We ignored extreme outliers (the top and bottom 0.1% of data) when setting bin widths. The algorithm generates distances to climate analogs; in keeping with Hamann et al. (2015), we redefined distances of zero as half the smallest possible non-zero distance and redefined non-analog distances as 10,000 km, before dividing distances by 33.5 years (the time between the midpoints of the two time periods) to derive velocities. Converting distances to velocities does not change the resulting spatial patterns, and was done for consistency with the literature. To minimize the effect of discrete bin boundaries, we evaluated velocity under four variants of the binning scheme each offset slightly in climate space and then averaged the results for each grid cell. Finally, velocities were log-transformed to support plotting and summarization.

2.8 | Summary analyses

Downstream analyses used EVT-based vegetation cover values in each grid cell when summarizing vulnerability metrics across types within a cell, or across cells within a single type's range. To summarize range-wide vulnerability of higher-level USNVC categories, we calculated mean vulnerability of grid cells occupied by any vegetation type within a category, weighted by percent cover within a cell. To explore how novelty varied within the geographic range of the average type, we converted climate and geographic coordinates into deciles within each type's range and then summarized these deciles across types.

All analysis was done in R version 3.5.1 (R Core Team, 2013), with geospatial and statistical tools from the raster (Hijmans, 2019), caret (Kuhn, 2018), and dismo (Hijmans, Phillips, Leathwick, & Elith, 2017) packages.

3 | RESULTS

3.1 | Climate variable importance

The relative importance of different climate variables differed across the 96 vegetation types (Figure 2; Figure S2). In the variable importance PCA (Figure 2a), PC1 primarily distinguished vegetation types influenced by summertime climate (five of the six variables with the largest positive PC1 loadings relate to climate in the warmest or

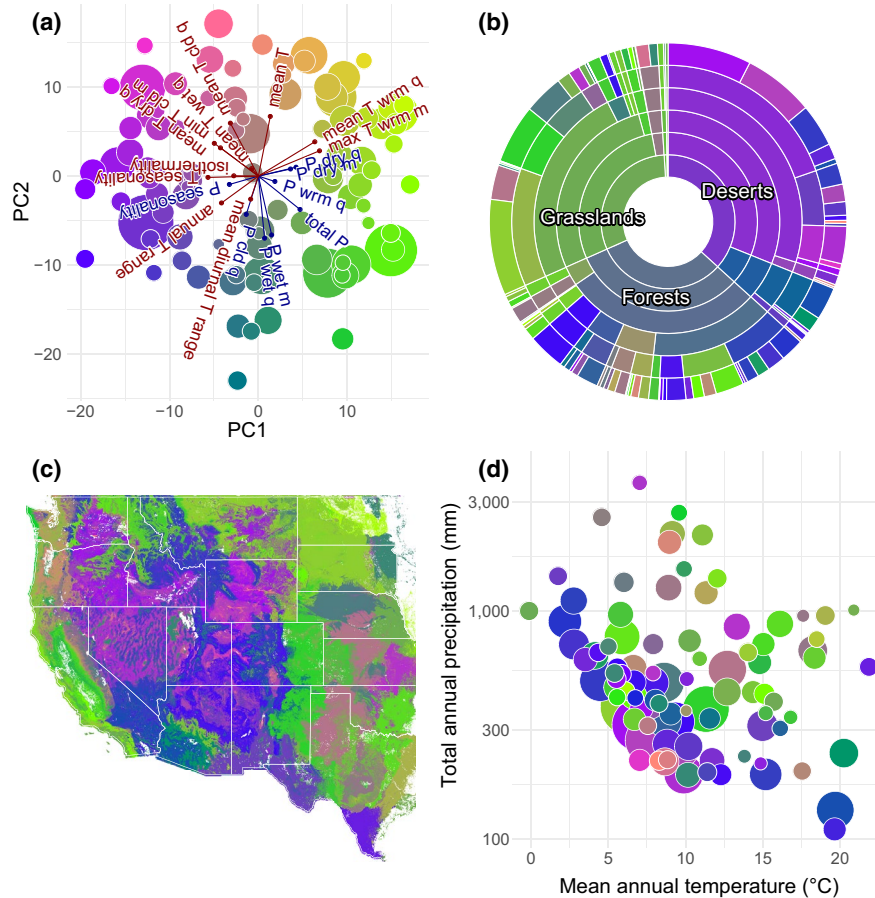


FIGURE 2 Geographic and ecological patterns in the climate variables most important to each vegetation type. (a) Vegetation types in variable importance space, based on ordination of the variable importance matrix—vectors indicate input variable importance loadings (m, month; P, precipitation; q, quarter; T, temperature; full definitions in Table S1), while points indicate vegetation types, with nearby types having distributions shaped by similar suites of variables; colors on this panel serve as the legend for other panels. (b) Variable importance across the vegetation classification (see Figure S1 for a labeled key); internal values are means of results for constituent vegetation types. (c) Geographic patterns of variable importance; grid cell values are means of local vegetation type PC scores, weighted by percent cover. (d) Variable importance across climate space, with points representing the mean annual temperature and precipitation across the range of each vegetation type. In all panels, color represents the set of climate variables important to each vegetation type as illustrated in (a). In (a), (b), and (d), point size and slice size are proportional to land area covered by a vegetation type within the study area

driest times of year) versus vegetation types influenced by winter-time climate (seven of the eight variables with the largest negative PC1 values relate to cold-season variables or to variables describing seasonality, which indirectly reflects winter extremes). PC2 primarily distinguished temperature- versus precipitation-influenced vegetation types (9 of 12 temperature variables loaded positively onto PC2, while all strong PC2 loadings for precipitation variables were negative).

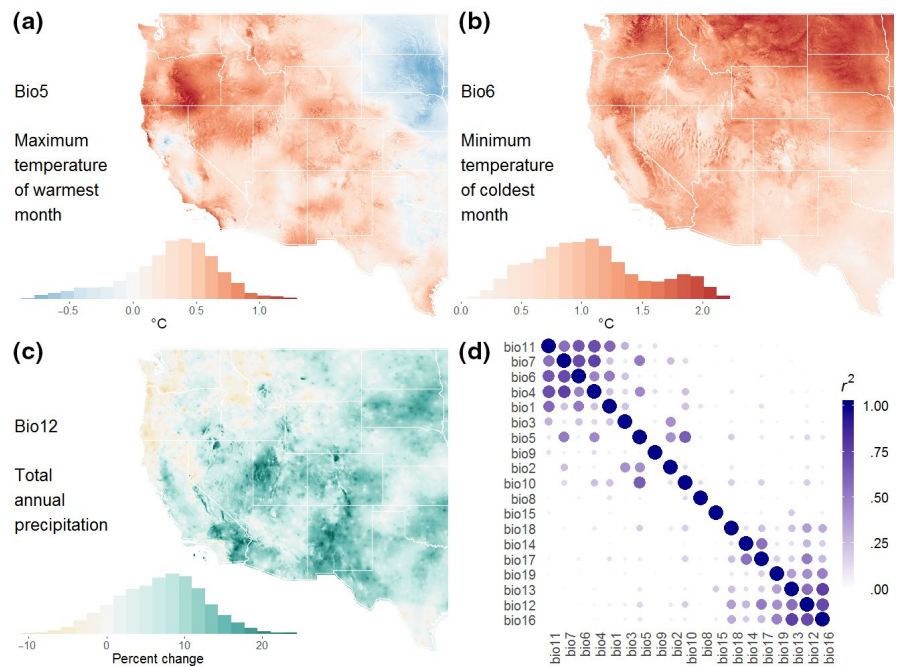
These PC scores indicate strong geographic and ecological patterns of climate sensitivity. Variable importance was hierarchically clustered across vegetation types, with similar types tending to share sensitivity to similar climate variables (Figure 2b). Desert and semi-desert vegetation tended to be most influenced by winter-seasonality-related variables, whereas shrub and herb vegetation tended to be most limited by precipitation and summer temperature gradients; forests and woodlands were less consistent in their climate sensitivities (Figure 2b). Across geographic space and climate

gradients, vegetation types in the Intermountain West and in colder and/or drier regions tended to be delimited by temperature-related and winter-seasonality-related variables; vegetation along the Pacific coast, the cordilleras, and the Great Plains—regions with relatively warmer and/or wetter mean annual climates—tended to be informed by gradients of precipitation and summer temperatures (Figure 2c,d).

3.2 | Climate change exposure

Rates of recent multidecadal climate change varied geographically, including across nearby locations, generating a mosaic of exposure patterns (Figure 3a–c). For example, mean annual precipitation changes varied from -10% to $+20\%$ across the region, and changes in minimum temperature of the coldest month varied from near zero to more than $+2^{\circ}\text{C}$. Furthermore, these geographic exposure patterns

FIGURE 3 Geographic variation in climate change exposure, defined as the difference in mean climates between the 1948–1980 baseline and 1981–2014 recent time periods. (a–c) Geographic variation in exposure for maximum temperature of the warmest month, minimum temperature of the coldest month, and total annual precipitation, respectively. (d) Pairwise correlations in exposure for the 19 bioclimate variables (defined in Table S1), illustrated as a heat map of the squared bivariate Pearson's correlations of exposure values across grid cells in the study area; point size and opacity indicate r^2



differed substantially among climate variables: in a PCA of exposure values for the 19 bioclimatic variables across the western US, 10 principal components were required to capture 95% of the total variance. This variation is further illustrated by bivariate correlations among exposure values for the 19 variables (Figure 3d), which show that most variables are changing relatively independently of one another across the region, although some subsets of variables did have highly correlated exposure patterns. These bivariate correlations between exposure values were only modestly predictable from correlations between baseline means ($r^2 = .40$), indicating that spatial associations among climate variables are being restructured with climate change. In sum, these results show that locations across this region experienced a highly diverse, individualistic set of climate change signatures that cannot be effectively summarized by a small number of representative climate variables.

3.3 | Vulnerability dimensions

The three metrics of climate change vulnerability—niche novelty (decline in suitability), temporal novelty (standardized climate anomaly), and spatial novelty (inbound climate velocity)—yielded distinct vulnerability estimates across various dimensions of the dataset (Figure 4; Figures S5 and S6). Grid cells of individual vegetation types had a mean (minimum/median/maximum) niche novelty of 0.09 (0.00/0.03/0.99) across the region, with the largest possible value of 1 representing a change from maximum suitability to zero suitability. Average temporal novelty was 0.23 (0.00/0.18/1.00), with the largest possible value of 1 indicating that the recent multivariate mean was more extreme than any individual year in the baseline. Mean spatial novelty (calculated after converting infinite distances to 10,000 km) was 2.77 (0.00/0.28/infinite) km/year, with

infinite values indicating locations with no analog climate in North America.

When we ranked grid cells according to the mean vulnerability of local vegetation for each of the three metrics, we found that most three-dimensional combinations of high and low vulnerability quantiles were present across some portion of the western US (Figure 4; Figure S5), indicating that these novelty dimensions are non-redundant and ecosystems are likely to experience diverse regimes of departure from baseline climate patterns. While most locations had some combination of high and low novelty values across the three measures, pockets of the Great Plains and Madrean Desert were among areas ranked as relatively highly vulnerable according to all three measures, whereas areas including parts of central Oregon, northeastern Colorado, and central Texas had relatively low exposure for all measures (Figure 4a). Niche and spatial novelty tended to be greatest in the east, whereas temporal novelty tended to be greatest in the central and southwest regions of the study area, though all regions exhibited major variation at finer scales.

Across the 96 vegetation types, mean range-wide vulnerability scores were relatively independent for the three metrics, with niche novelty and temporal novelty very weakly negatively correlated and both very weakly positively correlated with temporal novelty (Figure S6). These mean vulnerability values were clustered on the vegetation classification hierarchy, with similar types often exhibiting similar vulnerability for a given metric. Spatial novelty was most extreme among shrub and herb vegetation types (which are primarily grasslands), whereas temporal novelty was most extreme among forest and desert vegetation types; niche novelty exhibited little hierarchical structure (Figure S6).

We also found vulnerability trends across geographic and climate gradients at multiple scales (Figure 4). At broad

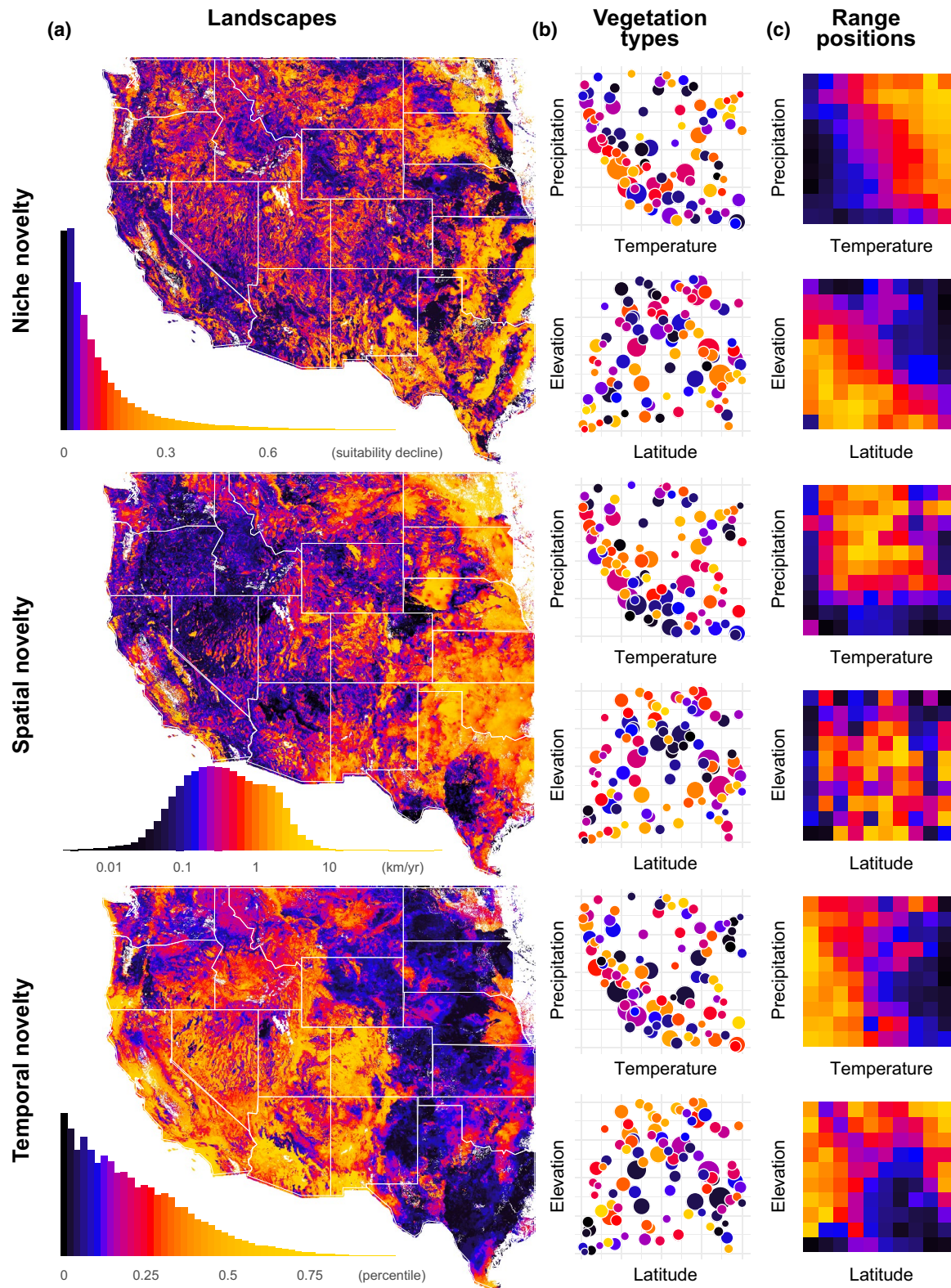


FIGURE 4 Vegetation climate change vulnerability across the western US according to three metrics of vulnerability: niche novelty, spatial novelty, and temporal novelty. (a) Mean novelty across all vegetation types in each grid cell, with histograms indicating frequencies of novelty values. (b) Mean range-wide novelty of vegetation types in climate and geographic spaces, with point size indicating the range size of each type. (c) Novelty as a function of a site's position within the geographic or climatic range of a vegetation type, averaged across all types. All colors represent percentiles within a sub-panel, with warmer colors indicating higher relative vulnerability. Figure S5 shows the multivariate combinations of these novelty metrics

scales comparing the mean vulnerabilities of vegetation types (Figure 4b), no novelty metric had clear relationships with latitude, but niche and spatial novelty were highest in lower-elevation vegetation types while temporal novelty was highest in higher-elevation types. Niche and spatial novelty also tended to be higher in warm-wet and cold-dry regions than in warm-dry or cold-wet regions. Patterns also emerged at smaller scales within the range of the typical vegetation type (Figure 4c). Niche vulnerability tended to be highest at the warm, wet edge of a type's distribution along the low elevation and low latitude margins, whereas temporal vulnerability was higher in colder high-elevation and low-latitude portions of a type's range; spatial vulnerability exhibited indistinct patterns with respect to within-range spatial gradients but tended to be lowest at warm, cool, and/or dry range edges.

The trend toward higher temporal novelty at higher elevations is consistent across 14 of the 19 climate variables, as measured by correlations between univariate standardized anomalies and altitude (Figure S7). This was a function of lower interannual climate variability at higher elevations for almost every variable (17 of 19) as well as higher exposure magnitudes at higher elevations for a subset of the variables (8 of 19, including the broadly important temperature variables Bio1, Bio5, and Bio6).

4 | DISCUSSION

In this study, we examined multiple aspects of climate change vulnerability across the geographic ranges of more than ninety vegetation types of the western US. This represents to our knowledge the first systematic comparison of niche-, spatial-, and temporal-based novelty paradigms, as well as an important advance in inferring patterns of climate variable importance and their influence on projected vulnerability patterns. Our findings offer new lessons about the relative climate vulnerability of vegetation communities and the landscapes they occupy, and highlight a range of vulnerability signatures that have distinct management implications for climate adaptation across these sites. Our focus on observed recent climate change helps to highlight the fine-scale spatial heterogeneity of multivariate climate trends and their potential implications for biodiversity in ways that future models cannot, though future models of course remain critical tools for ecological forecasting. While our analysis was focused on vegetation types, we stress that many of our findings should apply at other scales of the biotic hierarchy, from genes to species to biomes.

We identified a surprisingly diverse mosaic of climate change vulnerability profiles across the region's plant communities (Figure 4). This spatial heterogeneity was a function of three key underlying drivers: (a) highly variable rates of climate change itself, (b) differences among locations and vegetation types in the importance of different climate variables, and (c) relatively independent vulnerability patterns across the three metrics.

4.1 | Rates of climate change are highly heterogeneous

The first of these three drivers is largely extrinsic to vegetation and instead simply reflects the complex geophysics of climate change. Our results add to those of other studies (Rapacciuolo et al., 2014) in showing that different climate variables are changing at very different rates in different places (Figure 3), a phenomenon likely driven by interactions among nested macro-, meso-, and topo-scale climate feedbacks. Spatial heterogeneity in even a single variable can generate large exposure differences across landscapes (e.g., minimum temperature of the coldest month has increased more than 2°C since the mid-20th century in some landscapes but barely at all in others), and has been invoked as an explanation for diverse ecological responses to recent climate change (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011). Add to this our finding that such exposure patterns are largely uncorrelated among climate variables, likely driven by their contrasting relationships with geophysical gradients and their influences on one other, and a picture emerges of a high-dimensional exposure space in which each landscape is experiencing a relatively unique manifestation of climate change, with exposure signatures often differing strongly even among nearby sites.

One definition of a climate change refugium is a location in which climate changes less quickly than the surrounding region, helping buffer the local biota against the most rapid rates of change (Ashcroft, Chisholm, & French, 2009; Morelli et al., 2016). Our results corroborate previous studies in highlighting that such refugia tend to occur at multiple scales, and in different locations for different climate variables. These patterns highlight the importance of landscape-scale heterogeneity (Ashcroft et al., 2009) that would be masked by the low spatial resolution and significant uncertainties inherent in future GCM simulations. This reinforces the value of studying observed recent climate trends at relatively high spatial resolution as a complement to coarser future model predictions. Whether emerging fine-scale spatial patterns in recent climate change magnitudes will increase or decrease in the future as global climate change progresses remains an open and critically important question (Maclean, Suggitt, Wilson, Duffy, & Bennie, 2016).

4.2 | Strong climate variable importance trends shape vulnerability

The second major driver of heterogeneous climate vulnerability was spatial and ecological variation in the importance of different climate variables. Variable importance patterns are an aspect of the 'sensitivity' component of climate change vulnerability, shaping how vegetation types are projected to respond to a given magnitude of climate exposure. Broad-scale patterns in the importance of different climate variables have been underexplored, and while several recent studies have begun to examine variation

in the importance of different climate variables across species (Barbet-Massin & Jetz, 2014; Bradie & Leung, 2017; Schuetz et al., 2019), ours is the first to our knowledge to assess how such variation is structured spatially and ecologically. Our results present a first systematic look at broad-scale variable importance patterns for terrestrial vegetation, revealing patterns relevant both to basic ecology and to global change.

We found strong patterns of variable importance across geographic space, climatic gradients, and vegetation classes (Figure 2). The PCA of importance scores suggested that vegetation types can be primarily characterized as limited by either summer or winter conditions, and as limited by either temperature or precipitation variables. Desert shrubland vegetation types occupying the cool, dry Intermountain region at the center of the study area tended to be most sensitive to temperature and winter climate, whereas grasslands were more sensitive to precipitation and summer climate, with forest vegetation types having a more diverse set of limiting factors. These results imply that the key climatic variables relevant to vulnerability assessments differ across contexts, and offer a first look at factors predicting these differences.

Even if all locations experienced identical climate exposure, variable sensitivity patterns would generate heterogeneous ecological impacts because some species will be more sensitive to the variables that are changing fastest. In reality, we found that these variable importance patterns interacted with the highly non-uniform exposure patterns described above to generate even more spatially heterogeneous vulnerability patterns. This implies that tailoring climate vulnerability assessments to locally important variables can strongly influence results, and underscores the importance of ecological knowledge about the sensitivity of local ecosystems to different aspects of climate. These results stress that refugia are likely to differ among vegetation types and among species, depending on overlap between climate variables changing most slowly in different locations and those that are important influences on each vegetation type.

4.3 | Vulnerability estimates differ markedly by novelty paradigm

The third aspect of heterogeneous vulnerability was differences among the three novelty paradigms, each of which is based on a different reference distribution for what is considered the historical and normative baseline for a given ecosystem. All three metrics are based on the same exposure and variable importance inputs for a given vegetation type in a given site, and novelty for all three metrics is thus expected to correlate positively with the exposure magnitude of locally important variables. Given the strong patterns in exposure and variable importance common to all three metrics, and given a prior study that found concordance between niche models and future climate change metrics for African vertebrates (Garcia et al., 2016), we expected that our vulnerability metrics might also be strongly correlated and that any differences

among them might emerge only as second-order distinctions. Instead, we found that the three metrics were highly divergent, each identifying distinct landscapes and vegetation types as most and least vulnerable to climate change. Niche-based vulnerability and spatially based vulnerability exhibited a weak negative correlation across vegetation types, and both were only weakly positively correlated with temporal-based vulnerability. This multidimensionality of vulnerability metrics based on relatively fine-scale regional patterns of observed recent climate change adds empirical weight to similar patterns that have been forecast based on modeled coarser-resolution global data for the future (Garcia et al., 2014).

Detailed patterns of vulnerability across the three novelty metrics included both confirmations of common narratives as well as unexpected patterns. The three metrics showed striking differences in which edges of a given vegetation type's realized niche and geographic range they implicated as most threatened on average, as well as in which vegetation types they implicated as most threatened overall. Niche novelty was highest at warm, wet climate edges for the typical type, corresponding to the low-elevation, low-latitude margins of the type's distribution—an expected pattern that is in keeping with the narrative of upward- and poleward-shifting ranges in warming climates, which has been widely though inconsistently observed in field studies over recent decades (Rumpf et al., 2018; Wiens, 2016). Interestingly and more unexpectedly, we also found that low-elevation vegetation types had higher average niche novelty overall across their ranges. This broader-scale pattern represents a second relatively independent aspect of niche-based vulnerability in lower-elevation terrestrial ecosystems.

Spatial novelty, measured as inbound climate velocity, was generally highest for vegetation types in relatively low-elevation sites in the eastern portion of the study area and lowest for types inhabiting cool, dry landscapes of the intermountain region; these broad patterns largely agree with prior studies (Belote et al., 2018; Dobrowski et al., 2013). Within the geographic range of the typical vegetation type, inbound climate velocities were also low in dry areas and relatively high on the wet range edge, an expected pattern when climates are becoming wetter: all else equal, locations whose climate is more extreme in the direction that climate is changing (e.g., relatively wetter locations when precipitation is increasing) will tend to have higher inbound velocities. Velocities also tended to be lowest near both the warm and cool range margins, which could be driven by the tendency of climatically marginal populations to occur in isolated microclimates nested in topographically complex landscapes with low climate velocities.

In contrast to these metrics, temporal novelty was typically highest in colder, higher-elevation portions of a type's distribution, as well as in higher-elevation vegetation types overall. While temporal novelty is a function of both exposure magnitude and year-to-year variability, the data suggest that the latter component is the primary cause of the observed higher novelty at higher elevations. While higher elevations had higher exposure for many important temperature variables,

in keeping with prior studies showing modest positive relationships between elevation and temperature trend magnitudes after carefully controlling biases (Oyler, Dobrowski, Ballantyne, Klene, & Running, 2015), precipitation variables tended to change faster at lower elevations. However, the large majority of both temperature and precipitation variables exhibited lower year-to-year variability at higher elevations, ultimately leading to a clear pattern of higher temporal novelty at higher elevations. It remains uncertain whether this result is driven by an elevation-mediated climate dynamic per se—it could also result from higher-elevation areas tending to occur in regions that have high temporal novelty across all elevations, or could be an artifact of climate interpolation (if higher-elevation sites have lower spatial autocorrelation in their temporal climate anomalies, then climate surfaces interpolated from high-elevation stations could exhibit artificially dampened temporal variation). Further study is needed addressing mountain climate change dynamics, including at scales finer than the broad patterns reported here.

4.4 | Novelty signatures suggest distinct management approaches

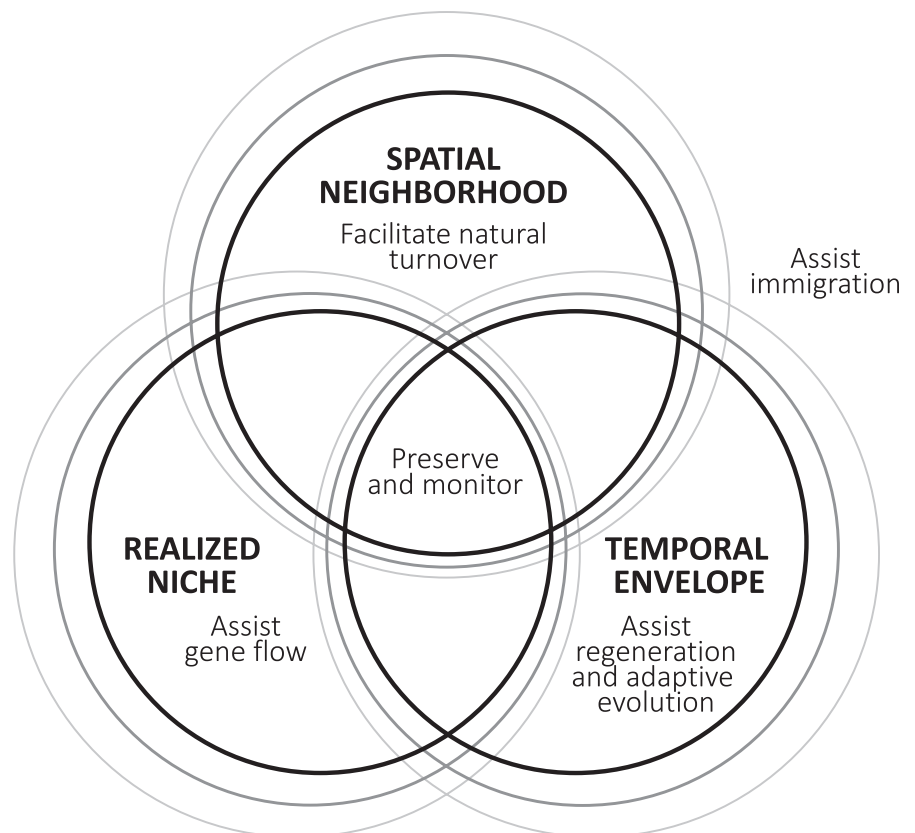
Each of these conceptually and empirically distinct novelty paradigms offers a hypothesis about the vulnerability of a given local population or ecosystem based on a particular model of resilience to climate change. While the metrics can be considered additive in the sense that higher vulnerability on any axis may mean a higher likelihood of ecosystem change or collapse under climate change, a richer

management perspective may come from considering the three metrics jointly. A given site will fall somewhere in the three-dimensional vulnerability space defined by these novelty metrics (Figure S5), different regions of which we argue are associated with distinct management strategies for climate adaptation (Figure 5).

When novelty is low in all three dimensions, intervention is not a priority and a relatively hands-off strategy of protecting and monitoring local populations may be warranted. The vegetation types most exemplifying this pattern across their ranges were certain coniferous forest types of the Sierra Nevada and Cascade mountains and shrubland types of the Intermountain Basin, though pockets of low vulnerability were present in many landscapes across the study area. Sites with this vulnerability signature may be important as climate refugia due to low rates of climate change, steep spatial climate gradients, or resilient vegetation.

When novelty is high in some dimensions but not others, different forms of intermediate-intensity intervention may be required to facilitate climate adaptation in the local ecosystem. If climate novelty for a site is high on the spatial and temporal dimensions but remains within the realized range-wide niche of the species or vegetation type, it raises the possibility that local genotypes or community members may be ill-adapted to the new climate and that future movement of adapted genes from nearby sites (or in situ adaptive variation from historic local gene flow) is unlikely. In this scenario, assisted gene flow from other parts of focal species' ranges may be warranted as a way to maintain population fitness in the locally novel climate (Aitken & Whitlock, 2013). While the rationale for assisted gene flow often assumes that plant populations are evolutionarily

FIGURE 5 Potential management approaches to climate change adaptation for populations or ecosystems with different combinations of climate novelty values across the three metrics. High novelty or vulnerability for a given dimension is represented as a site's new climate being outside the circle encompassing the baseline climate distribution that defines a given vulnerability metric. For example, a population with low niche novelty but high spatial and temporal novelty would be located within the species realized niche but outside the local spatial neighborhood and the historic temporal envelope, and could be a target for assisted gene flow. Management strategies for the empty two-way intersections could represent more subtle combinations of the approaches listed for adjacent regions. Concentric circles reflect the notion that these novelty metrics are continuous rather than binary designations



adapted to their local historic environments—a pattern that is common but not ubiquitous (Hereford, 2009)—assisted gene flow can also help facilitate evolutionary adaptation even in the absence of local adaptation by increasing genetic diversity (Aitken & Whitlock, 2013). High levels of historical gene flow could also lead to maintenance of adaptive genetic variation within populations (Sork et al., 2010), even if conditions depart from the historical climate distribution. Field studies are needed to determine the degree of local adaptation and levels of adaptive genetic variation within populations.

Where niche and spatial novelty are both high but temporal novelty remains relatively low, gene flow or natural turnover are unlikely to maintain ecological function but local populations have some demonstrated ability to survive the new mean climate. This scenario is common at low-elevation range limits and across large tracts of the Great Plains in the eastern portion of the study area, both geographies that tend to have relatively high year-to-year climatic variation that may have facilitated local adaptation to a wider range of climates. Under these conditions, the management priority may be to bolster the fitness of local populations by facilitating adaptive evolution and assisting with regeneration, which is often the limiting demographic stage if the juvenile recruitment niche is more restrictive than the adult tolerance niche (Grubb, 1977; Jackson, Betancourt, Booth, & Gray, 2009). Interventions in this scenario might include seeding and artificial selection, as well as more broadly applicable strategies like reducing non-climatic ecological stressors such as grazing and invasive species that are widespread across the study area.

If spatial novelty is low but both niche and temporal novelty are high, local populations of the focal species may be unsustainable but nearby sites are likely to contain climatically suitable species that could disperse and establish in the focal site, adaptively maintaining ecosystem function by filling ecological roles left by extirpated species. Managers in such cases may wish to facilitate this natural turnover using approaches such as maintaining or restoring connectivity among natural vegetation patches, employing prescribed fire where appropriate to reduce competition and speed establishment of newly suitable species, or performing localized assisted migration to jumpstart populations. In these situations, assisted migration may involve only local-scale movement of propagules, reducing concerns about introduction of exotic species. However, facilitating vegetation change may still raise concerns that historical baselines are being lost unnecessarily, challenging long-established norms for priority setting in conservation (Hobbs et al., 2014).

High vulnerability in all three novelty dimensions indicates that intensive management intervention may be required to prevent ecosystem collapse. This novelty signature was found across pockets of the Great Plains, the Madrean desert, the Rocky Mountains, and the Pacific coast. With the new mean climate outside the range of historic variation experienced by the local population, outside the range of mean climates across the entire distribution of the type, and outside the range of climates found in the nearby area surrounding the focal site, local populations may be unsustainable and viable alternatives may be lacking from nearby communities. Longer-distance assisted immigration—importing species that have

desirable ecological attributes and are adapted to current or future climates—has been recommended under such circumstances as a means to maintain ecosystem structure and function (Hoegh-Guldberg et al., 2008). While controversial, assisted migration may play an increasing role in the adaptation toolkit as climate exposure and its ecological impacts continue to grow (Richardson et al., 2009).

It is important to carefully consider the concepts and assumptions that underlie each novelty metric when evaluating vulnerability, as the dimensions may be more or less relevant for a given species or vegetation type. For example, temporal novelty may provide more insight than niche novelty where local adaptation or non-climatic distributional constraints are thought to be important, and spatial novelty may be less relevant than other metrics in highly dispersal-limited systems where natural immigration is unlikely. Thus, while phylogenetic or ecological traits may be imperfect as direct predictors of climate vulnerability as discussed above (Buckley & Kingsolver, 2012), they could prove much more informative in determining the relevance of different vulnerability paradigms. For instance, niche model success in predicting range shifts is associated with plant species traits (Dobrowski et al., 2011), and characteristics like dispersal ability shape the influence of spatial novelty on paleoclimatic range shifts (Sandel et al., 2011).

Integrating these multiple vulnerability paradigms with additional ecological knowledge may thus offer a way forward in understanding and predicting individualistic responses to climate change. Macroecological-scale data are now widely available on ecological traits and on recent trends in population sizes and range limits. We call for further studies to assess which of the niche, temporal, and spatial novelty paradigms best explain observed biodiversity trends under what ecological circumstances, and to do so using frameworks that consider the high-dimensional nature of climate exposure and incorporate variation in sensitivity to these climate dimensions.

ACKNOWLEDGEMENTS

This work was funded by a grant from the US Bureau of Land Management to HH. MK was supported in part by a US National Science Foundation Graduate Research Fellowship. We thank Colin Mahony and two additional anonymous reviewers for insightful feedback that helped to improve and clarify this manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Kling MM, Auer SL, Comer PJ, Ackerly DD, Hamilton H. Multiple axes of ecological vulnerability to climate change. *Glob Change Biol.* 2020;26: 2798–2813. <https://doi.org/10.1111/gcb.15008>