PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Scale-dependent complementarity of climatic velocity and environmental diversity for identifying priority areas for conservation under climate change

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Funding information
Wilburforce Foundation

Abstract

As most regions of the earth transition to altered climatic conditions, new methods are needed to identify refugia and other areas whose conservation would facilitate persistence of biodiversity under climate change. We compared several common approaches to conservation planning focused on climate resilience over a broad range of ecological settings across North America and evaluated how commonalities in the priority areas identified by different methods varied with regional context and spatial scale. Our results indicate that priority areas based on different environmental diversity metrics differed substantially from each other and from priorities based on spatiotemporal metrics such as climatic velocity. Refugia identified by diversity or velocity metrics were not strongly associated with the current protected area system, suggesting the need for additional conservation measures including protection of refugia. Despite the inherent uncertainties in predicting future climate, we found that variation among climatic velocities derived from different general circulation models and emissions pathways was less than the variation among the suite of environmental diversity metrics. To address uncertainty created by this variation, planners can combine priorities identified by alternative metrics at a single resolution and downweight areas of high variation between metrics. Alternately, coarse-resolution velocity metrics can be combined with fine-resolution diversity metrics in order to leverage the respective strengths of the two groups of metrics as tools for identification of potential macro- and microrefugia that in combination maximize both transient and long-term resilience to climate change. Planners should compare and integrate approaches that span a range of model complexity and spatial scale to match the range of ecological and physical processes influencing persistence of biodiversity and identify a conservation network resilient to threats operating at multiple scales.

KEYWORDS
climate change adaptation, climatic velocity, conservation planning, environmental diversity, land facets, protected areas, refugia

1 | INTRODUCTION

As most regions of the earth transition to altered climatic conditions in the coming decades (Mora et al., 2013), climate-driven shifts in biomes, species, and ecosystem processes will make conservation plans based on current patterns of biodiversity less effective (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). Data commonly used in conservation planning, such as the distributions of ecological communities or land cover types, may lose efficacy as surrogates for their component species as those species respond individualistically to climate change. This problem has stimulated a search for new types of metrics that can better inform conservation planning under climate change.

To be effective in the face of climate change, networks of conservation areas must protect climatic refugia, habitats that components of biodiversity retreat to, persist in, and potentially expand from under changing climatic conditions (Keppel et al., 2012). More generally, planners need to prioritize conservation of areas that maximize landscape-level adaptive capacity, that is, areas whose conservation would disproportionately facilitate persistence of biodiversity and ecosystem function under climate change. The refugia concept is scale-dependent, in that macrorefugia (areas where broad-scale climate is suitable for persistence) are distinct from microrefugia (small areas with locally favorable environments within otherwise potentially unsuitable climates) (Reside et al., 2014).

The many approaches that have been suggested for identifying refugia (Table S1) can be distinguished based on three information axes (space, time, and species ecology (or "self" sensu) Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012). Approaches that delineate potential refugia by identifying areas of high environmental diversity consider variation across space (Ackerly et al., 2010; Ashcroft, Gollan, Warton, & Ramp, 2012). In contrast, approaches based on climatic velocity consider both spatial and temporal information (Figure 1). Climatic velocity, a metric based on either historical or projected future climate, estimates the rate at which organisms must move across the surface of the earth to stay within similar climatic conditions (Carroll, Lawler, Roberts, & Hamann, 2015; Loarie et al., 2009). Areas with low projected climatic velocities may act as refugia because the species in those areas will have to move only short distances to track changes in climate. Lastly, metrics such as biotic velocity (the rate at which organisms must move to stay within the climatic niche of their species) additionally consider the third axis (species-specific ecological information) (Carroll et al., 2015; Ordonez & Williams, 2013).

The pros and cons of using different types of data to identify refugia hinge in part on the trade-off between model uncertainty and complexity (here defined based on conceptual and computational complexity and the number and types of input data required rather than by spatial and temporal resolution or other factors). In theory, metrics derived from climatic niche models or mechanistic viability models (Keith et al., 2014), which integrate all of the three information axes described above, would most accurately identify locations of species refugia (Figure 1). However, the complexity of
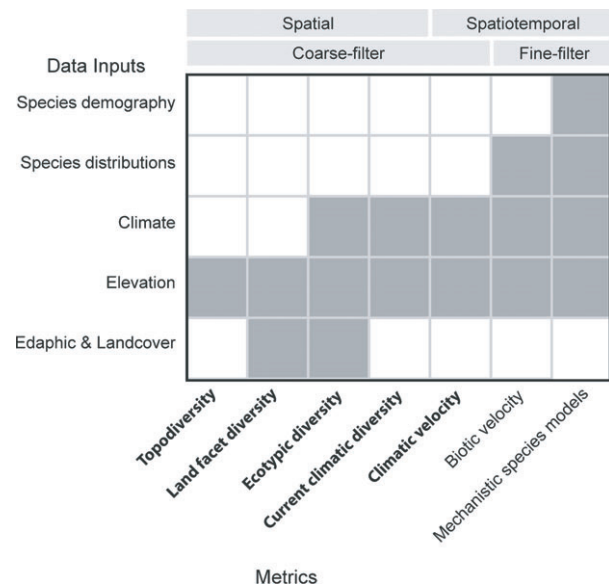
Definitions of metrics used in this study

Topodiversity: Degree of variation, within a spatial neighborhood around each cell (pixel), in elevation or heat load index (a metric based on aspect and slope).

Land facet diversity: Diversity, as measured by the Gini-Simpson index, which represents the probability that two cells from the neighborhood of interest represent different classes of land facet types based on soil order, elevation, landform, and heat load index.

Ecotypic diversity: Gini-Simpson index values derived from an ecotype classification based on climate, landform, lithology, and landcover type.

Current climatic diversity: Degree of variation, within a spatial neighborhood around each cell, in climate represented as a multivariate distance based on 11 bioclimatic variables.

Climatic velocity: Distance in multivariate climate space between a cell and the nearest cell with matching climate in the future.

FIGURE 1 Categorization and definition of a selection of alternative metrics proposed for use in refugia identification in terms of their use of spatial or spatiotemporal information and use of nonspecies-specific (coarse-filter) or species-specific (fine-filter) data. A variety of more complex methods and metrics for refugia identification are not shown in the figure

these models also brings increased model uncertainty, as well as data requirements that may limit their application to a subset of a region's biota. Additionally, use of a nonspecies-specific metric such as climatic velocity may allow a more comprehensive analysis, and may provide information on the degree of threat to locally adapted populations rather than species (Carroll et al., 2015).

Use of environmental diversity metrics represents an even simpler, and thus potentially more generalizable, approach to identifying potential refugia. Topographic diversity (topodiversity) may be useful for identifying areas where a heterogeneous physical environment (e.g., steep elevation gradients or diverse aspects) increases the likelihood that species will be able to find nearby suitable habitat as climate changes. Species distributions, communities, ecosystems, and broader patterns of biodiversity are clearly influenced by abiotic drivers such as soils, geology, and topography. Stein, Gerstner, and Kreft (2014), in a meta-analysis of 192 studies, found that heterogeneity in land cover, vegetation, climate, soil, and topography were all positively correlated with species richness, with vegetation and topographic heterogeneity showing particularly strong associations.

An approach in which conservation priorities are based on abiotic land classifications and associated environmental diversity metrics has been termed "Conserving Nature's Stage" (Anderson et al., 2015; Beier, Hunter, & Anderson, 2015; Comer et al., 2015; Lawler et al., 2015). This approach is motivated by several premises: (i) physical habitat types are effective coarse-filter (nonspecies-specific) surrogates for biological diversity; (ii) the influence of soils, geology, and topography in creating habitat variation is likely to persist as climates change; (iii) physical habitat data are more robust to uncertainty than metrics based on future climate projections, which vary dependent on the atmosphere-ocean general circulation model (AOGCM) and emission scenario considered; and (iv) use of physical habitat data facilitates planning because these data are easier and cheaper to develop than spatiotemporal metrics (Beier, Hunter, et al., 2015). This approach, in addition to prioritizing areas of high environmental diversity, may also seek to ensure adequate representation of all physical habitat types ("land facets", i.e., land classifications derived from soils and topography; Figure 1) in a conservation network, based on the hypothesis that protecting a diversity of physical habitat types will foster a diversity of biota in the future, albeit different biota than those areas would protect today (Beier, Hunter, et al., 2015). Although individual sites may not function as refugia in the typical sense under this hypothesis, the conservation network as a whole is hypothesized to be resilient in terms of its ability to maintain components of biodiversity under climate change (Anderson et al., 2015). Consideration of representation goals also helps fulfill the long-recognized principle that priority areas should be well distributed across the landscape (Scott et al., 2001).

Recent reviews have suggested that planners use alternative metrics that span a range of complexity to overcome the shortcomings of individual approaches (Garcia, Cabeza, Rahbek, & Araujo, 2014; Gillson, Dawson, Jack, & McGeoch, 2013). Many previous studies have used environmental diversity data along with spatiotemporal metrics as part of a multi-objective prioritization process (Table S1). Game, Lipsett-Moore, Saxon, Peterson, and Sheppard (2011) developed a national climate adaptation strategy for Papua New Guinea that sought to simultaneously capture areas with (i) low dissimilarity between current and future environmental space, (ii) high environmental heterogeneity, and (iii) a diversity of geophysical habitat types. Ashcroft et al. (2012) identified a network of refugia in New South Wales, Australia using metrics based on topoclimate, climatic stability, and isolation from the matrix. Groves et al. (2012) suggested an approach that combined representation of geophysical types, protection of refugia as identified from climate data and topodiversity, and conservation of habitat connectivity. Gillson et al. (2013) suggested that planners use a suite of modeling methods including both species-based models and those based on representation of physical habitat.

Reside et al. (2014) identified refugia based on climatic velocity, species-specific climatic niche models, compositional-turnover modeling (Ferrier, Manion, Elith, & Richardson, 2007), areas of stable vegetative productivity during drought events ("greenspots"; Mackey et al., 2012), and areas of connectivity between current and future refugia. Tingley,

Darling, and Wilcove (2014) proposed the use of conservation targets based on natural elements unaffected by climate change (e.g., physical habitat types) and locations with low climatic velocity. Lastly, Schmitz et al. (2015) proposed a framework which integrated six objectives: (i) protect current patterns of biodiversity, (ii) forecast future patterns of biodiversity, (iii) maintain ecological processes, (iv) maintain and restore ecological connectivity, (v) protect climatic refugia, and (vi) protect the "ecological stage" (physical habitat types).

While the metrics considered here can be used to suggest potential refugia, we cannot test their ability to predict the location of biotic refugia under future climates, due in part to irreducibly uncertain parameters such as the rate of future anthropogenic emissions. Our goal is to compare these two types of widely used metrics rather than to compare their accuracy with that of more complex metrics such as species niche models. Ultimately, the most relevant type of metric and resolution of data will depend on the goals and spatial scale of the planning effort.

Although the use of environmental diversity metrics in planning appears promising in principle, we still know little about the origins and implications of the commonalities and contrasts between alternative metrics. In this study, we compared prioritization approaches that targeted areas of high environmental diversity or low climatic velocity, either with or without consideration of how these values were distributed across landscape types. Although we focus on North America due to our involvement in conservation planning efforts there, we hypothesize that our general conclusions will be transferable to other continents.

Specifically, we asked the following questions:

1. How different are solutions (networks of conservation priority areas) based on alternative metrics, and are the patterns of contrasts correlated with regional characteristics such as elevation, latitude, temperature, or precipitation?
2. Does the ability of simpler metrics to serve as surrogates for more complex metrics vary across scales, and does the additional goal of ensuring priorities are represented across landscape types increase or decrease these contrasts?
3. What level of uncertainty characterizes metrics such as velocity which are based on climate projections, and how does this uncertainty compare with variation among diversity metrics?
4. How do solutions that capture both microrefugia (identified using high-resolution environmental diversity metrics) and macrorefugia (identified using coarser-resolution velocity metrics), and ensure that such areas are well distributed across a spectrum of landscape types, compare in terms of efficiency and overlap with solutions based on fewer objectives?

Although alternative approaches to climate-aware conservation planning have been proposed previously, they have not been compared across a range of ecoregions in order to draw general conclusions concerning how surrogate performance varies with ecological context. Our results contribute to a better understanding of when and how to use simple and more complex metrics for identifying

refugia, and help build an evidence-based foundation for development of systematic conservation planning focused on climate resilience and adaptive capacity.

2 | MATERIALS AND METHODS

2.1 | Comparison of environmental diversity and velocity metrics

We developed and compared six metrics (elevational diversity, heat load index [HLI] diversity, current climatic diversity, ecotypic diversity, land facet diversity, and backward climatic velocity; Figure 1, Table S2) that have been proposed as tools for assessing landscape-level adaptive capacity and vulnerability.

We derived the metrics across North America (Fig. S1), to draw more comprehensive and generalizable conclusions by comparing metrics across a diverse set of ecoregions that vary widely in their topographic and climatic attributes. We also sought to evaluate how the ability of simpler metrics to serve as surrogates for more complex metrics varied across scales. To support this evaluation, the six diversity metrics were derived at three resolutions (1, 3, and 9 km) and three window widths (3, 9, and 27 km). Climatic velocity, which lacks a window extent parameter, was developed at four resolutions (1, 3, 9, and 27 km).

The diversity metrics are examples of neighborhood or "moving window" metrics based on summary statistics derived from the set of cells within the spatial neighborhood of each focal cell. In contrast, the velocity metric is based on a nearest-neighbor function which searches over the entire extent of the data to identify the most spatially proximate cell that "matches" the focal cell based on the attribute of interest (Carroll et al., 2015; Hamann, Roberts, Barber, Carroll, & Nielsen, 2015). Diversity metrics based on larger window extents were more analogous to velocity in this respect. We therefore focused primarily on the comparison of velocity against diversity metrics with the largest window extent (27 km) with a resolution (1 km) that matched that of the highest resolution velocity metric.

2.2 | Topography-based metrics: elevational and HLI diversity

Elevation data for North America were assembled from SRTM v4.1 (Farr et al., 2007) below 60°N latitude, and ASTER GDEM v2 (ASTER GDEM Validation Team, 2009) above 60°N. Data were resampled to 100 m resolution from an original resolution of 1 arc-second (~30 m) (ASTER) to 3 arc-second (~90 m) (SRTM). Higher resolution (30 m) SRTM data (v4.2) are now available, and would be preferable for analyses at regional extents. However, 30 m resolution diversity analyses at continental extents are computationally challenging, and 90 m SRTM v4.1 data resampled to 30 m showed high (>.99) correlation with 30 m STRM v4.2 data.

We also converted elevation data to HLI (McCune & Keon, 2002). HLI, a metric based on slope, aspect and latitude, is an estimate of the potential annual direct incident radiation at a location that is related to

microclimatic diversity in a different manner than is elevation. We derived elevational and heat load diversity values using a form of Rao's quadratic entropy, by measuring the mean Euclidean environmental distance (e.g., elevation or HLI) between all pairs of cells within a spatial neighborhood defined by the moving window of the specified extent (3, 9, or 27 km) (Ackerly et al., 2010; Rao, 1982).

2.3 | Current climatic diversity

The HLI diversity metric effectively assumes that heterogeneous topography will result in heterogeneous climates. Alternately, one can directly assess the level of modeled climatic heterogeneity within a spatial neighborhood under current climatic conditions. Although current climatic diversity is characteristic of a specific time period, we characterize it as a spatial rather than spatiotemporal metric because it does not incorporate a rate of change over time. We calculated a current climatic diversity metric using climate data for a recent 30-year climate normal period (1981–2010), interpolated to 1 km resolution using the CLIMATENA software (Wang, Hamann, Spittlehouse, & Carroll, 2016). CLIMATENA climate data are based on climate rasters developed by the PRISM project, which uses a regression approach to interpolate weather station data based on location, elevation, coastal proximity, topographic facet orientation, vertical atmospheric layer, topographic position, and orographic effectiveness of the terrain (Daly et al., 2008). CLIMATENA downscales PRISM grids using a lapse rate dynamically developed based on local grids for each monthly temperature and precipitation variable.

We used 11 secondary bioclimatic variables more directly related to ecological factors (Table S3), which are calculated by the CLIMATENA software from the monthly temperature and precipitation data (Wang, Hamann, Spittlehouse, & Murdock, 2012). Wang, Hamann, et al. (2012) and Wang, Hamann, Spittlehouse, and Carroll et al. (2016) identified key bioclimatic variables based on the previous studies concluding that these variables were important in ecological models (e.g., models separating forest ecosystems in British Columbia and the western United States; Rehfeldt, Crookston, Warwell, & Evans 2006; Wang, Campbell, O'Neill, & Aitken, 2012).

We used principal components analysis to reduce the dimensionality of the 11 climate variables, which eliminated collinearity for subsequent stages of the analysis. Our Rao's quadratic entropy metric was based on multivariate Euclidean climate distance using the first 4 PCA axes, which accounted for 97% of total variance in the 11 climate variables.

2.4 | Class-based metrics: land facet and ecotypic diversity

We also assessed environmental diversity based on categorical variables which had been used to classify the landscape into distinct units (Table S4). Landscape units derived from topographic and soil or geologic data have been termed "land facets" (Beier & Brost, 2010). We developed data categorizing the North American continent into land facets at 100 m resolution and aggregated the data to

the 1, 3, and 9 km resolutions based on the majority of 100 m classes within the larger grid cells. Land facet classes were derived from categorical variables representing elevation and HLI (as described above), as well as landform and soil order (see Appendix S1 for details of classification system).

As an alternative to a classification that relies purely on physical features, we used ecological land units (ELU), which Sayre et al. (2014) derived from growing degree days, an aridity index, landform, lithology, and land cover type. We derived land facet and ecotypic diversity using the Gini-Simpson diversity index (Jost, 2006). Comparison of land facet and ecotype diversity provides information on how diversity-based priorities differ when derived from two systems of land-type classification, one based purely on physical features and a second that also incorporates climate and land cover data.

2.5 | Climatic velocity

The velocity of climate change, as originally proposed by Loarie et al. (2009), is derived by dividing the temporal rate of projected climate change by the rate of climate variability across a spatial neighborhood. Here we used an alternative velocity algorithm that extends the search for climate refugia across the entire continent to directly estimate the distance between a location and the nearest location with similar climate in the future (Hamann et al., 2015). Future projected temperature and precipitation were calculated as anomalies from the current (1981–2010) reference period to the future 2071–2100 period (hereafter "2080s"), based on an ensemble mean of 15 representative CMIP5 AOGCMs included within CLIMATENA. Anomaly grids were downscaled via local regression and the difference was added to the baseline climate normal data to arrive at the final climate surface (Wang et al., 2016).

We used climate data based on the first two axes of the principal components analysis of 11 climate variables described above. We used equally spaced intervals of 0.25 PCA units to divide current and future climate space into multivariate bins. To eliminate artifacts due to bin boundaries, we incrementally offset bin boundaries over 100 replicated velocity calculations and averaged the results. For each unique climate type (bin), we identified cells (pixels) within that type under both current and projected climates. Then, we used fast approximate nearest neighbor algorithms (from R package yaImpute; Crookston & Finley, 2008) to identify, for each future cell, the nearest cell of the same type under current climates. This metric, termed backward climatic velocity, represents the distance and rate at which organisms adapted to a location's future climate will need to move to reach that location. As such, it represents a measure of a location's ability to serve as a refugium (Carroll et al., 2015). In contrast, the more typically encountered climatic velocity metric, forward velocity, is more relevant to measuring threats to organisms themselves, as it represents the rate at which an organism currently at a location must move to find future suitable climate. For use in identifying networks of conservation priority areas (as described below), we used the negative logarithm of velocity to create a metric comparable to the diversity metrics, in that higher values identified areas with higher refugia potential.

2.6 | Testing correlation and concordance between metrics

Before assessing the spatial concordance between priority areas identified by alternative metrics, we first evaluated the correlation between the metrics themselves using several methods. Firstly, we calculated the Spearman correlation coefficients between the six metrics, which had been calculated across a range of resolutions and analysis windows. Secondly, we divided the range of velocity values into quantiles, and evaluated whether the correlation between diversity and velocity varied between low and high velocity areas. We used generalized additive models (GAM) to evaluate how the six metrics varied with respect to elevation.

We created linear regression models with climatic velocity as the dependent variable and the diversity metrics as independent variables. We then performed commonality analysis (Ray-Mukherjee et al., 2014) on the linear regression models to evaluate the unique and shared contributions of each of the diversity metrics to explaining patterns of velocity. We also tested the correlation between velocities derived from different AOGCMs and emissions scenarios (representative concentration pathways, RCP), to evaluate the degree of uncertainty originating from these factors. For this subset of analyses, we also compared the more distant future projection (2071–2100, or "2080s") used throughout the study with a near future projection (2041–2070, or "2050s").

2.7 | Identification of priority area networks using the ZONATION software

The degree of correlation between environmental diversity and velocity metrics provides important information but does not directly translate to applications where networks of priority areas (here termed "solutions") are selected based on systematic conservation planning principles (Margules & Pressey, 2000). Therefore, we also compared and contrasted alternative solutions based on diversity and velocity metrics (Table 1).

We identified solutions using the ZONATION software (Moilanen, 2007; Moilanen et al., 2005). ZONATION produces a hierarchical ranking of conservation priorities over the entire landscape, based on principles of complementarity. Lowest ranks are given for grid cells whose deletion minimally effect the total conservation value retained within the solution because they do not contain a high value of any metric. Highest ranked cells include the highest values of multiple metrics. Areas with highest rank would be retained longest as a successively smaller proportion of the landscape is retained within a protected area system.

We used ZONATION's core-area-based prioritization option, which emphasizes solutions that collectively include high-quality locations for all conservation features. Core-area ZONATION is most appropriate when, as here, the goal is to protect all conservation targets rather than assume trade-offs between targets (Moilanen, 2007). Although ZONATION runs used a resolution of 3 km for computational feasibility at the continental analysis extent, we found that solutions were

TABLE 1 Goals for alternative solutions (networks of conservation priority areas) identified using the ZONATION software

Solution	Target	Spatiotemporal	Multi-objective	Representation-based
Group 1—Single objective solutions				
1	Areas of high elevational diversity			
2	Areas of high heat load diversity			
3	Areas of high current climate diversity			
4	Areas of high ecotype diversity			
5	Areas of high land facet diversity			
6	Areas of low backward climatic velocity	×		
Group 2—Multi-objective solutions				
7	Areas maximizing 1–6 above	×	×	
Group 3—Representation-based solutions				
8	Areas of low backward climatic velocity represented across climate types	×	×	×
9	Areas of high land facet diversity represented across land facet types		×	×
10	Areas fulfilling both 8 and 9 above	×	×	×
Group 4—Multiscale representation-based solutions				
11	Areas fulfilling both 8 and 9 above, using within-cell diversity	×	×	×

similar at varying resolutions (e.g., >.97 correlation between 3 and 9 km resolutions).

We developed four types of solutions (numbered as Groups 1–4 in Table 1): (i) single-objective solutions, which sought to maximize the total value of a single diversity or velocity-based metric (e.g., protect potential areas of highest elevational diversity or low velocity); (ii) multi-objective solutions, which sought to simultaneously capture high value areas based on several diversity or velocity metrics; (iii) representation-based solutions, which sought to maximize areas of high diversity or low velocity within all landscape types (climatic and/or land facet types); and (iv) multiscale representation solutions, which sought to maximize areas of high diversity or low velocity (potential macrorefugia) within all landscape types, while also prioritizing potential microrefugia, that is, areas with high topographic diversity below the grain of the solution.

The value of systematic conservation planning software lies in optimizing priorities based on multiple conservation features. In real-world planning contexts, ZONATION solutions would not be based on a single feature because this set of priority areas could be identified using simpler tools. We include single-objective solutions in this comparison because (i) they allow a comparison with multi-objective solutions using identical methods; and (ii) they simplify calculations which seek to identify the highest value areas in each of many administrative units (e.g., ecoregions).

2.8 | Ecoregions as strata and climatic regions as representation targets

We opted to stratify representation targets by ecoregion (CEC, 1997) to approximate the typical extent of planning processes and allow us to evaluate how the pattern of contrasts between alternative solutions varied by ecoregion (n = 182; Fig. S2a). We characterized this pattern of contrasts based on each ecoregion's mean and standard deviation of elevation, latitude, annual temperature, annual precipitation, and continentality (expressed as the difference between mean temperature of coldest and warmest month).

For a subset of solutions, we used climatic regions as a representation target. The climatic regions were delineated using a maximum-likelihood-based unsupervised classification of North America into 495 regions based on the first four principal components of a PCA based on 11 bioclimatic variables (Table S3) under current climate (Fig. S2b). Representation by climatic region distributed low-velocity priority areas (potential macrorefugia) throughout current climatic space, with the goal of conserving biota adapted to all current climates.

2.9 | Comparison of priority area solutions

We evaluated the similarity of ZONATION solutions based on two metrics: (i) the cross-correlation coefficient (Goodchild, 1986) between rasters representing the rank (priority) assigned in the ZONATION results to each cell of the landscape, and (ii) the Species Accumulation Index (SAI; Rodrigues & Brooks, 2007), which compares the amount of a feature captured in solutions focused on the feature itself with the amount captured in solutions based on alternate features (surrogates). SAI is calculated from the ratio (S–R)/(O–R), with S being the amount of a metric captured within the surrogate-based solution, O being the optimum value captured in the feature-based solution, and R being the mean value captured in a randomly selected solution (Beier et al., 2015). SAI ranges from negative infinity to 1, with negative SAI corresponding to a worse than random result, 0 indicating random performance, and positive SAI representing a measure of effectiveness (Beier & De Albuquerque, 2015).

We also created linear regression models to evaluate the ability of ecoregion-level characteristics (elevation, latitude, temperature, precipitation, and continentality) to explain the cross-correlation between the landscape rankings produced by alternate solutions. Lastly, we evaluated the performance of the current system of protected areas in North America (IUCN categories 1(strict nature reserve)—6 (sustainable use area); C.E.C., 2010) in representing areas prioritized in the ZONATION solutions by measuring the mean rank of cells within and outside of the current protected area system.

3 | RESULTS

3.1 | Commonalities and contrasts between metrics

Elevational, HLI, and current climatic diversity formed a group of closely correlated metrics ($\bar{x}$ of Spearman's rank correlation (ρ) = .89 across all resolutions and window extents; Fig. S3). Land facet diversity was moderately correlated with these three metrics ($\bar{x}$ of ρ = .69). Ecotypic diversity was the most distinct of the diversity metrics ($\bar{x}$ of ρ = .55 with all other diversity metrics). The diversity metrics showed increased correlation among themselves as grain and/or window extent increased (Fig. S3).

Rankings derived from diversity metrics based on continuous variables were relatively robust to choice of scale (both resolution and window extent) (Fig. S4). However, diversity metrics based on categorical variables (ecotypic and land facet diversity), although robust to choice of resolution, showed only moderate correlation ($\rho \geq .53$) between values measured at different window extents, due to influence of rare landscape types on diversity values. The contrast between backward climatic velocity and the diversity metrics was greater than any contrast among the diversity metrics themselves. At 1 km resolution and 27 km window extent, velocity was correlated similarly with all diversity metrics (ρ = .36–.40) except land facet diversity (ρ = .29).

3.2 | Sensitivity of velocity values to contrasts between AOGCMs, RCPs, and time periods

Velocity metrics derived from different AOGCMs were relatively highly correlated ($\bar{x}$ of ρ = .74; Fig. S5). This level of correlation is greater than that between the diversity metrics as a whole ($\bar{x}$ of ρ = .70). Correlation between AOGCMs increased slightly between the near future and distant future (2050s and 2080s) projections as the warming signal came to dominate the "noise" of AOGCM model uncertainty (Fig. S6).

Correlation between velocity metrics based on different RCPs was also relatively high ($\bar{x}$ of ρ = .85; Fig. S6), although correlation decreased between near future and distant future projections. Correlation between rankings based on near-future and distant-future velocity was relatively high ($\bar{x}$ of ρ = .88), but contrasts between time periods were greater for the extreme emissions scenario (RCP 8.5) than for the moderate scenario (RCP 4.5).

3.3 | Contrasting relationship of diversity and velocity metrics to elevation

Low-elevation areas, which were generally also the flattest areas (ρ of elevation and slope = .53 at 1 km resolution), showed the lowest values for all metrics (Figure 2). Although all diversity and velocity metrics showed a broadly similar relationship with elevation below 2,000 m, they diverged at higher elevations. Elevational and HLI diversity showed the strongest positive correlation with elevation across all elevation values (Figure 2a), suggesting that, at least in North America, the highest mountain regions are also most topographically diverse. Ecotype and land facet diversity showed lowest correlation with elevation. The relationship of current climatic diversity with elevation was intermediate to that of the two previous groups. The refugia metric derived from backward climatic velocity showed correlation with elevation similar to those shown by current
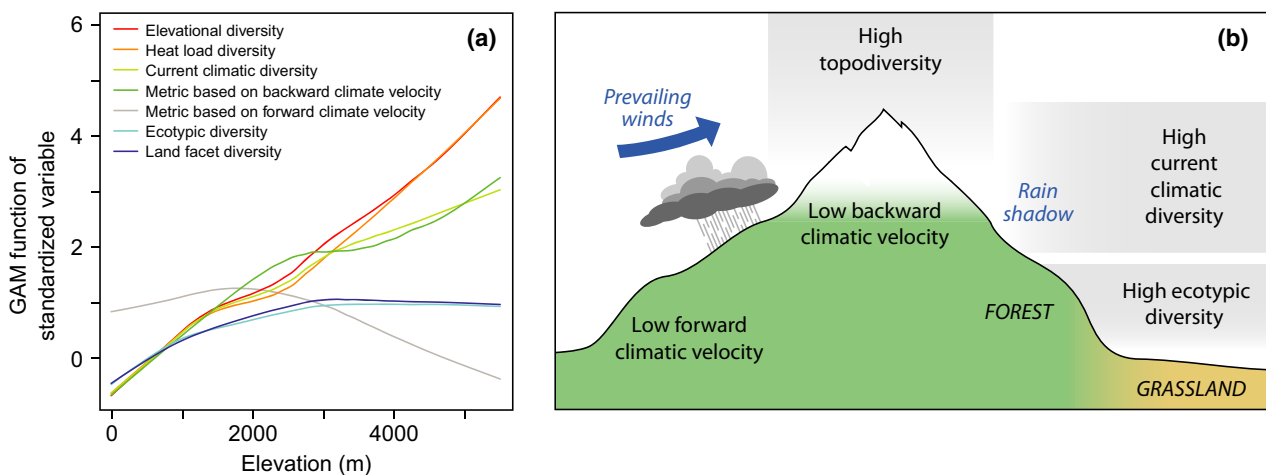

FIGURE 2 Contrasts between diversity and velocity metrics in their relationship with elevation zones: (a) generalized additive model of relationship between metrics and elevation across North America, (b) conceptual figure indicating elevational zones showing high values of the various metrics. Forward climatic velocity is shown for comparative purposes but is not further analyzed in the study

climatic diversity, but with greater emphasis on mid-elevations (Figure 2).

3.4 | Scale dependent correlation between diversity and velocity

Correlation between diversity and velocity also varied between low and high velocity areas. The rank correlation of elevational diversity and negative log velocity at 1 km resolution and 27 km window extent was .38 overall, but increased to .60 for those areas with velocity values of < 5 km/year (Fig. S7). Maximum correlation with velocity was lower for diversity metrics with coarser resolutions or smaller window extents (Fig. S7).

We applied commonality analysis (Ray-Mukherjee et al., 2014) to a regression of climatic velocity on the diversity metrics, both for the full range of velocity values and for refugial areas with velocities of <2.25 km/year. This threshold was chosen because such refugia represented a proportion of the continent approximately equivalent to the extent of the current protected areas system (10.2%). For a regression based on all areas, current climatic diversity showed greatest unique contribution to the model, but most of the model's explanatory power was shared between elevational, HLI, and current climatic diversity (Fig. S8a). The unique contribution of elevational diversity increased and that of current climatic diversity decreased when the regression focused on variation within low velocity refugia (<2.25 km/year) (Fig. S8b). Model fit was low ($r^2 < .19$) for both models.

3.5 | Comparison of ZONATION solutions

For single-objective solutions (Fig. S9), both the species accumulation index (SAI) values (Figure 3) and cross-correlation of priorities (rank of removal from ZONATION solution; Fig. S10) between elevational, HLI, and current climatic diversity were high ($\bar{x} = .87$ and .81, for SAI and correlation, respectively). In contrast, priorities based on ecotypic and land facet diversity had only moderate SAI and correlation ($\bar{x} = .58$ and .57, respectively) with other diversity metrics. Priorities based on climatic velocity showed low SAI and correlation ($\bar{x} = .34$ and .39, respectively) with all diversity metrics. A multi-objective solution based on the six diversity and velocity metrics (Figures 4 and Fig. S11) performed moderately well for all targets ($\bar{x} = .55$ and .65 for SAI and correlation, respectively). Note that, unlike cross-correlation values, SAI values are not symmetrical in that the surrogacy value of metric A for metric B may not equal that of metric B for metric A (Figure 3).

Solutions designed to capture areas of low backward climatic velocity represented across climate types (solution 8; Table 1) correlated poorly ($\rho = .27$) with priorities designed to capture areas of high land facet diversity represented across land facet types (solution 9) (Fig. S11). Additionally, use of landscape-level representation targets (climate zones or land facet types) or strata (ecoregions) resulted in artificially high priorities at type or strata boundaries.

However, a multi-objective solution based on both climatic and land facet representation goals (solution 10) correlated moderately well with priorities based on climate types or land facet types alone

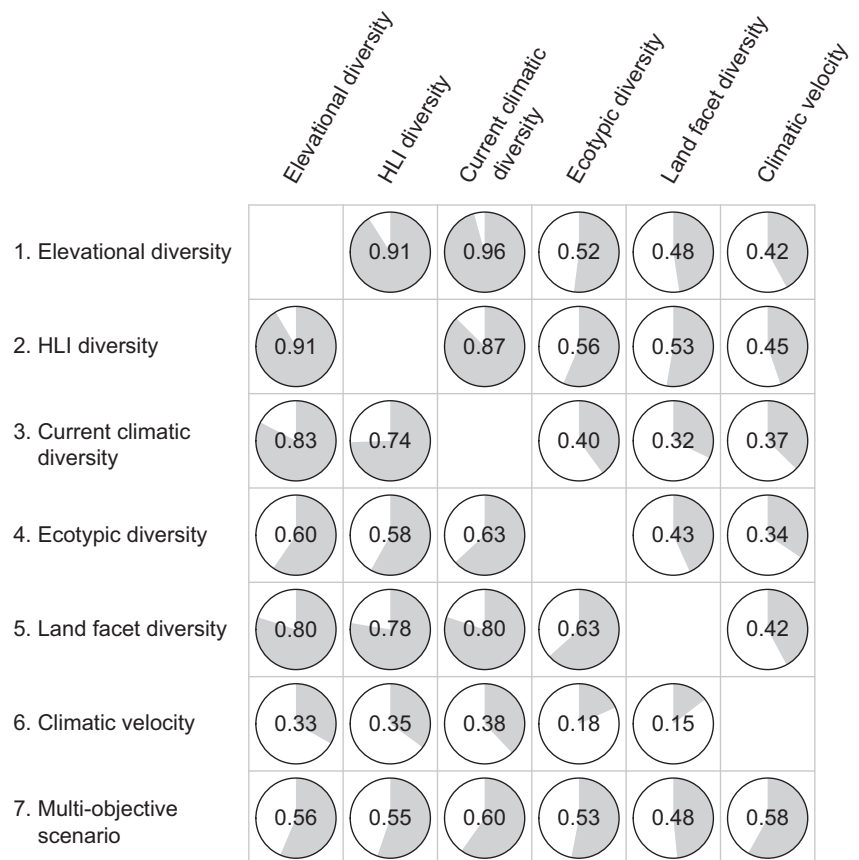|	Elevational diversity	HLI diversity	Current climatic diversity	Ecotypic diversity	Land facet diversity	Climatic velocity
1. Elevational diversity		0.91	0.96	0.52	0.48	0.42
2. HLI diversity	0.91		0.87	0.56	0.53	0.45
3. Current climatic diversity	0.83	0.74		0.40	0.32	0.37
4. Ecotypic diversity	0.60	0.58	0.63		0.43	0.34
5. Land facet diversity	0.80	0.78	0.80	0.63		0.42
6. Climatic velocity	0.33	0.35	0.38	0.18	0.15	
7. Multi-objective scenario	0.56	0.55	0.60	0.53	0.48	0.58

FIGURE 3 Species accumulation index (SAI) values representing the ability of single- and multi-objective ZONATION solutions (numbered 1–7 as in Table 1) to capture high-value areas for six different metrics, relative to an optimal and random solution
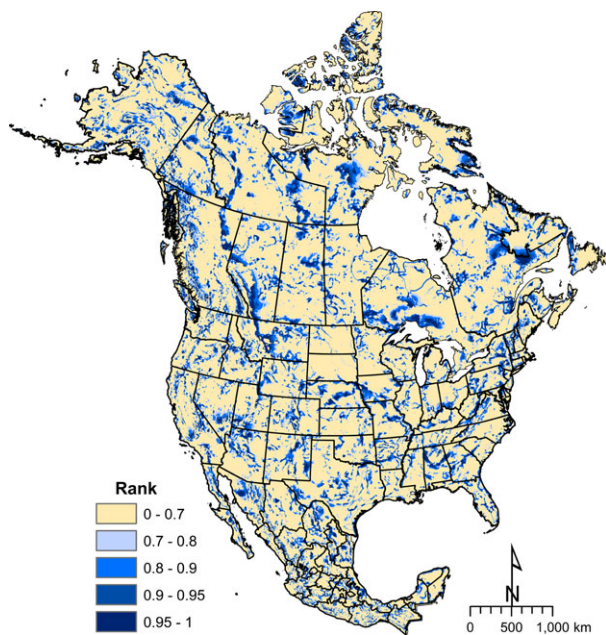
FIGURE 4 Conservation priority ranking for North America based on a multi-objective ZONATION solution (scenario 7; Table 1) capturing areas of high importance based on six diversity and velocity metrics [Colour figure can be viewed at wileyonlinelibrary.com]

(ρ = .61 and .75, respectively). Multiscale priorities based on both climatic and land facet representation goals, but incorporating within-cell land facet diversity (solution 11), were highly correlated with an analogous solution (solution 10) based on between-cell diversity (ρ = .89).

Linear regression models of the effect of ecoregional characteristics on the degree of correlation between priorities based on elevational diversity and velocity suggested that correlation was higher in lower elevation ecoregions with greater standard deviation in elevation (e.g., mountainous coastal regions). However, although the elevational variables were significant in the model ($p < .01$, $n = 182$ ecoregions), model r^2 was low (.07). The ecoregional characteristics evaluated here were not significant in predicting correlation of priorities between climatic and land facet representation goals (solutions 8 and 9).

3.6 | Performance of current protected area system

Protected areas in the dataset we used represented 10.2% of North America. The mean rank of the protected area system ranged from .52 to .59 across the various ZONATION solutions (Fig. S12). This suggests that the tendency of both protected areas and areas of high diversity to be located at higher elevations is not in itself sufficient to ensure that high diversity areas are captured within the current protected area system. Because many nonecological factors influenced where parks were created in the past, the overlap between existing protected areas and any systematic planning solution tends to be low. However, even a small difference between metrics is of practical significance given the large areas considered and the large

socioeconomic costs of new park designation. Priorities based on elevational, HLI, and current climatic diversity were captured to a greater degree in the current system of protected areas (mean rank within protected areas of .58–.59) (Fig. S12). In contrast, priorities based on ecotypic and land facet diversity and velocity were less well captured within protected areas (mean rank within protected areas = .54, .56, and .53, respectively). No metrics had mean rank values below .5, which would reflect conservation targets being found disproportionately outside protected areas. The differences in mean rank between the metrics are consistent with previous contrasts between metrics in terms of their relationship with elevation (Figure 2).

4 | DISCUSSION

Although many approaches have been suggested for identifying refugia and other areas whose conservation would facilitate species persistence under climate change, we still know little about the origins and implications of the commonalities and contrasts between alternative metrics. We compared several widely used approaches across a broad range of ecological settings in North America to determine how commonalities in the priority areas identified by different methods varied with ecological context and spatial scale. We found that priority areas based on different environmental diversity metrics differed substantially from each other and from priorities based on climatic velocity metrics. Our results highlight the need to better understand the implications of these contrasts for conservation planning under climate change.

The environmental diversity metrics that we considered fell into three groups in terms of their correlation with elevation (Figure 2). Priorities developed from the two topographic diversity metrics increased focus on high-elevation areas, which are already overrepresented in protected areas (Joppa & Pfaff, 2009; Scott et al., 2001; Tingley et al., 2014). In contrast, priorities derived from categorical landscape units rather than continuous variables distributed conservation priorities more broadly across elevation zones (Figure 2). Land facet and ecotypic diversity were similar in this effect, despite being based on different landscape classifications.

This contrast is partly due to both the incorporation of additional nontopographic inputs (edaphic, climatic, and land cover data) into the categorical metrics. Additionally, the ecologically informed class boundaries used to categorize the data, and the different index by which diversity was measured for categorical variables, contributed to shifting high diversity areas toward lower elevations. For example, low- to mid-elevation areas with high ecotypic diversity might include an ecotone originating from precipitation thresholds governing the shift from forest to grassland ecosystems (Figure 2b). However, the ability of such landscape classifications to predict refugia depends in part on whether these thresholds retain their relevance to biota under future climates. Metrics such as biotic velocity that incorporate future biotic thresholds avoid this assumption at the cost of increased model complexity.

TABLE 2 Spatial scale of the physical and ecological factors related to refugia value and adaptive capacity, and their influence on alternative metrics

		Diversity					Climatic velocity	Biotic velocity
		Elevational	HLI	Ecotype	Facet	Climate		
Cold air pooling	100 m							
Water accumulation								
Variation in insolation with aspect			×					
Temperature lapse rate with elevation		×		×	×		×	×
Orographic lift and rain shadow	1 km			×		×	×	×
Climatic thresholds driving ecotype transitions				×				×
Soil/geologic transitions					×			
Coastal proximity/maritime effects	10 km					×	×	×
Current broad-scale circulation patterns						×	×	×
Future shifts in circulation patterns							×	×
Latitudinal variation in insolation						×	×	×
Biogeographic barriers	>100 km							×

Both current climatic diversity and backward climatic velocity showed an intermediate relationship with elevation when compared to the two previous groups (Figure 2). These metrics are influenced by topography (due to use of topographic data in the statistical downscaling process) but also by broad-scale factors such as prevailing circulation patterns, coastal proximity, and orographic effectiveness of the terrain (Daly et al., 2008) (Table 2). Peak values of climatic diversity may, for example, occur in rain shadow areas on the leeward side of mountain tops (Figure 2b). Priorities based on these climatic variables may represent a useful compromise that avoids overemphasis on montane areas while acknowledging the value of the steep climatic gradients they support.

4.1 | How different are conservation networks based on alternative metrics, and do representation goals increase or decrease these contrasts?

Comparison of priority area networks based on single metrics confirmed that the different metrics are only weak surrogates for one another. The degree of contrast between metrics varied by ecoregion, but there were no strong patterns to contrasts. Generally, contrasts were greatest in interior plateaus, where patterns of velocity were dominated by broad-scale factors, and lowest in rugged coastal ecoregions where topographic influences dominated. Additional consideration of representation goals (climatic or land facet types) accentuated the contrasts between priority area networks based on different types of metrics.

Our results underscore the importance of considering the spatial scale of factors influencing alternative metrics (Table 2). The results of the commonality analysis suggest that while topodiversity and current climatic diversity had similar power in predicting velocity values for the data as a whole, velocity was predominantly influenced by gradients in topodiversity in lower velocity areas (Fig. S8), where

topodiversity and velocity gradients are more closely correlated (Fig. S7). In areas with high velocities, the correlation between diversity and velocity is low because velocity patterns are more strongly influenced by broad-scale factors such as projected shifts in synoptic weather patterns (Table 2). In low velocity areas, environmental diversity is more closely correlated with velocity because both are strongly influenced by factors such as temperature lapse rate with elevation.

4.2 | Limitations of coarse-filter and coarse-resolution metrics

Environmental diversity and climatic velocity are arguably the metrics most commonly proposed and used to identify potential refugia in climate adaptation planning (Schmitz et al., 2015; Tingley et al., 2014). The goal of this study is to compare these two types of metrics, rather than to compare their accuracy in identifying biotic refugia with the performance of more complex metrics such as species niche models. Conservation planning is always an exercise in decision making in the face of limited and uncertain data, and especially so in the case of planning for climate change. Planners should remain aware of the limitations of both diversity and velocity metrics in capturing complex biotic responses to climate change. Coarse-filter metrics such as we discuss in this study should typically be complemented with fine-filter (species-specific) metrics where that information is available (Tingley et al., 2014). Additionally, there are a variety of more complex methods for refugia identification based on climatic data that address connectivity, isolation, compositional turnover, and interannual variations in climate (e.g., frequency of extreme temperatures and drought) (Dobrowski & Parks, 2016).

Planners should also recognize that even when high-resolution topographic data are available, the types of metrics reviewed here cannot fully capture complex microclimatic patterns that determine the location of microrefugia (Table 2). The relationship between

topography and climate can also vary substantially across latitude and season, and between current and future climates (Mountain Research Initiative, 2015). Fine-scale microclimatic measurements from ground-based stations can better predict microrefugia (Meineri & Hylander, 2016), but the sparse coverage of such stations may limit their use in continental or regional analyses.

There has been recent progress in using remotely-sensed land surface temperature data to identify microrefugia. However, this data also has limitations in terms of spatial (MODIS) and temporal (Landsat) resolution (Pepin, Maeda, & Williams, 2016). Further work is needed using these remotely sensed data to validate diversity metrics derived from elevation data and improve the ability of climate downscaling methods to represent local climate. Due to the scale-related challenges inherent in refugia identification at the broad extents relevant to conservation planning, coarse-resolution metrics remain useful as a complement to high-resolution mapping of microrefugia at smaller extents.

4.3 | What level of uncertainty characterizes metrics based on temporal projections?

Recent reviews have proposed that abiotic variables may provide a more robust basis for identifying priorities under climate change because of the inherent uncertainty in projections of future climate arising from contrasts between AOGCMs and emission scenarios (Beier & Brost, 2010; Beier, Hunter, et al., 2015). However, in our results the level of uncertainty that characterized climatic velocity metrics was similar to that between closely related diversity metrics, and less than that among the suite of diversity metrics as a whole. While diversity metrics may have less inherent model uncertainty because they make few assumptions about future biotic responses to climate change, they miss important physical and ecological processes that are captured albeit imperfectly by velocity metrics (Table 2).

Systematic conservation planning tools such as the ZONATION software are designed to identify solutions that efficiently achieve multiple objectives (Moilanen, 2007). Rather than focusing on identifying a single "best" metric, planners can combine priorities identified by alternative coarse-resolution metrics, and use approaches such as info-gap discounting (Moilanen & Wintle, 2006) to downweight
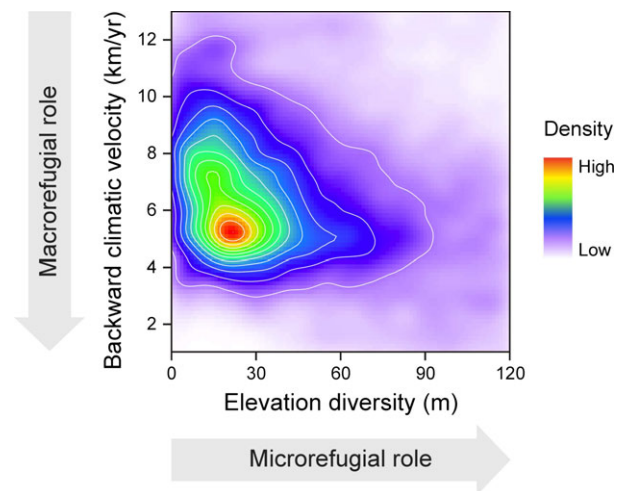

FIGURE 5 The bivariate distribution of elevational diversity and backward climatic velocity values for 1 km^2 cells (pixels) in North America, indicating their relative value as macro- (y-axis) and microrefugia (x-axis) [Colour figure can be viewed at wileyonlinelibrary.com]

areas of high variation between metrics. In our results, ZONATION showed moderate success in identifying networks of areas that were important in terms of both diversity and velocity (Figure 3).

Elevation data, because they are typically available at a much higher spatial resolution than climate data, are better suited than is climatic velocity for identifying microrefugia created by fine-scale processes (Table 2). Such high-resolution topographic data can be integrated with climatic data via an elevation-based statistical downscaling algorithm (Wang et al., 2016). However, as spatial resolution increases, limited additional information can be gained via statistical downscaling processes, and such processes become computationally challenging over large extents (Hall, 2014; Xie et al., 2015).

4.4 | Integrating diversity and velocity metrics in conservation planning

A more effective approach may be to first use coarse-resolution velocity metrics to identify potential macrorefugia. Fine-resolution topodiversity metrics can then be used to identify fine-scale microrefugia within and outside those macrorefugia (Figures 5 and
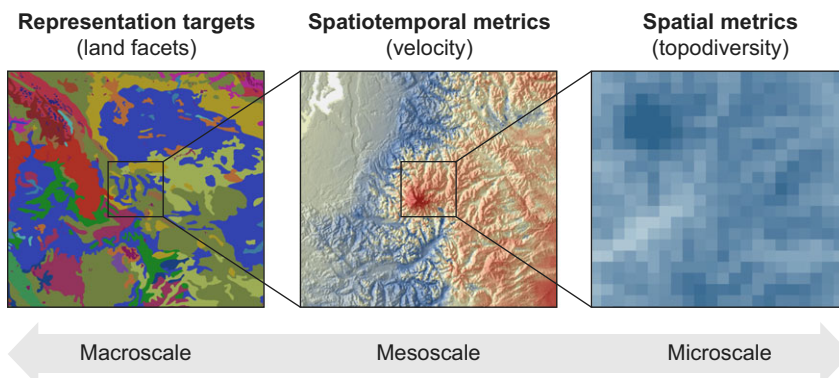

FIGURE 6 Conceptual diagram of a multiscale prioritization strategy for refugia identification and landscape-level adaptation planning. A network of priority conservation areas would be designed to capture high-diversity microrefugia within areas of low climatic velocity, distributed across landscape types

6). Additional high-resolution data on microclimatic gradients may also be used where available to capture processes poorly represented in downscaling algorithms (Dobrowski, 2011) (Table 2).

In this approach, diversity and velocity metrics, due to their inherent scale differences, form two distinct axes that are complementary tools for identification of micro- and macrorefugia, respectively (Figure 5). Identification of microrefugia alone will not result in a robust conservation network. Locations with high environmental diversity will play distinct roles depending on whether they lie within or outside of macrorefugia. In the latter context, microrefugia may form holdout or stepping stone habitat (Hannah et al., 2014) that has only transient value before being overwhelmed by broad-scale climate shifts.

Existing planning approaches often combine a focus on locations of high environmental diversity (potential microrefugia) with landscape-level representation goals (Anderson, Clark, & Sheldon, 2014). In North America, such analyses have been used recently to help guide conservation easements and land acquisitions by national conservation organizations and local land trusts (Anderson et al., 2015). Our results suggest that such approaches focused on microrefugia and representation can be strengthened by adding information on macrorefugia identified by climatic velocity metrics (Figure 6). By integrating data from approaches that span a spectrum of model complexity and spatial scale, conservation planners can better evaluate the range of ecological and physical processes influencing persistence of species and identify a conservation network resilient to threats operating at multiple scales.

ACKNOWLEDGEMENTS

REFERENCES

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. B. (2010). The geography of climate change: Implications for conservation biogeography. *Diversity and Distributions*, 16, 476–487.

Anderson, M. G., Comer, P. J., Beier, P., Lawler, J. J., Schloss, C. A., Buttrick, S., ... Faith, D. P. (2014). Estimating climate resilience for conservation across geophysical settings. *Conservation Biology*, 28, 959–970.

Anderson, M. G., Comer, P. J., Beier, P., et al. (2015). Case studies of conservation plans that incorporate geodiversity. *Conservation Biology*, 29, 680–691.

Ashcroft, M. B., Gollan, J. R., Warton, D. I., & Ramp, D. (2012). A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. *Global Change Biology*, 18, 1866–1879.

ASTER GDEM Validation Team (2009). *ASTER global DEM validation summary report*. METI & NASA, 28 pp. Retrieved from https://asterweb.jpl.nasa.gov/gdem.asp

Beier, P., & Brost, B. (2010). Use of land facets to plan for climate change: Conserving the arenas, not the actors. *Conservation Biology*, 24, 701–710.

Beier, P., & De Albuquerque, F. S. (2015). Environmental diversity as a surrogate for species representation. *Conservation Biology*, 29, 1401–1410.

Beier, P., Hunter, M. L., & Anderson, M. (2015). Special section: Conserving nature's stage. *Conservation Biology*, 29, 613–617.

Beier, P., Sutcliffe, P., Hjort, J., Faith, D. P., Pressey, R. L., & Albuquerque, F. (2015). A review of selection-based tests of abiotic surrogates for species representation. *Conservation Biology*, 29, 668–679.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, 15, 365–377.

Carroll, C., Lawler, J. J., Roberts, D. R., & Hamann, A. (2015). Biotic and climatic velocity identify contrasting areas of vulnerability to climate change. *PLoS One*, 10, e0140486.

C.E.C. (1997). *Ecological regions of North America towards a common perspective*. Montréal, QC, Canada: Commission for Environmental Cooperation.

C.E.C. (2010). *Terrestrial protected areas of North America, 2010*. Montréal, QC, Canada: Commission for Environmental Cooperation.

Comer, P. J., Pressey, R. L., Hunter, M. L., Schloss, C. A., Buttrick, S. C., Heller, N. E., ... Shaffer, M. L. (2015). Incorporating geodiversity into conservation decisions. *Conservation Biology*, 29, 692–701.

Crookston, N., & Finley, A. (2008). yaImpute: An R package for kNN imputation. *Journal of Statistical Software*, 23, 1–16.

Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., ... Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology*, 28, 2031–2064.

Dobrowski, S. Z. (2011). A climatic basis for microrefugia: The influence of terrain on climate. *Global Change Biology*, 17, 1022–1035.

Dobrowski, S. Z., & Parks, S. A. (2016). Climate change velocity underestimates climate change exposure in mountainous regions. *Nature Communications*, 7, 12349.

Farr, T. G., Rosen, P. A., Caro, E., Crippen, R., Duren, R., Hensley, S., ... Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, 45, RG2004.

Ferrier, S., Manion, G., Elith, J., & Richardson, K. (2007). Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. *Diversity and Distributions*, 13, 252–264.

Game, E. T., Lipsett-Moore, G., Saxon, E., Peterson, N., & Sheppard, S. (2011). Incorporating climate change adaptation into national conservation assessments. *Global Change Biology*, 17, 3150–3160.

Garcia, R. A., Cabeza, M., Rahbek, C., & Araujo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, 1247579.

Gillson, L., Dawson, T. P., Jack, S., & McGeoch, M. A. (2013). Accommodating climate change contingencies in conservation strategy. *Trends in Ecology & Evolution*, 28, 135–142.

Goodchild, M. (1986). *Spatial autocorrelation. Concepts and techniques in modern geography 47*. Norwich, UK: Geo Books.

Groves, C. R., Game, E. T., Anderson, M. G., Cross, M., Enquist, C., Ferdaña, Z., ... Shafer, S. L. (2012). Incorporating climate change into systematic conservation planning. *Biodiversity and Conservation*, 21, 1651–1671.

Hall, A. (2014). Projecting regional change. *Science*, 346, 1461–1462.

Hamann, A., Roberts, D. R., Barber, Q. E., Carroll, C., & Nielsen, S. E. (2015). Velocity of climate change algorithms for guiding conservation and management. *Global Change Biology*, 21, 997–1004.

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & Mccullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stones, and microrefugia. *Trends in Ecology & Evolution*, 29, 390–397.

Joppa, L. N., & Pfaff, A. (2009). High and far: Biases in the location of protected areas. *PLoS One, 4*, e8273.

Jost, L. (2006). Entropy and diversity. *Oikos, 113*, 363–375.

Keith, D. A., Akcakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., . . . Rebelo, T. G. (2014). Detecting extinction risk from climate change by IUCN Red List criteria. *Conservation Biology, 28*, 810–819.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., . . . Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography, 21*, 393–404.

Lawler, J. J., Ackerly, D. D., Albano, C. M., Anderson, M. G., Dobrowski, S. Z., Gill, J. L., . . . Weiss, S. B. (2015). The theory behind, and the challenges of, conserving nature's stage in a time of rapid change. *Conservation Biology, 29*, 618–629.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature, 462*, 1052–1055.

Mackey, B., Berry, S., Hugh, S., Ferrier, S., Harwood, T. D., & Williams, K. J. (2012). Ecosystem greenspots: Identifying potential drought, fire, and climate-change micro-refuges. *Ecological Applications, 22*, 1852–1864.

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405*, 243–253.

McCune, B., & Keon, D. (2002). Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science, 13*, 603–606.

Meineri, E., & Hylander, K. (2016). Fine-grain, large-domain climate models based on climate station and comprehensive topographic information improve microrefugia detection. *Ecography*, in press. doi: 10.1111/ecog.02494

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. *Biological Conservation, 134*, 571–579.

Moilanen, A., Franco, A. M., Early, R. I., Fox, R., Wintle, B., & Thomas, C. D. (2005). Prioritizing multiple-use landscapes for conservation: Methods for large multi-species planning problems. *Proceedings Biological Sciences, 272*, 1885–1891.

Moilanen, A., & Wintle, B. A. (2006). Uncertainty analysis favours selection of spatially aggregated reserve networks. *Biological Conservation, 129*, 427–434.

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., . . . Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature, 502*, 183–187.

Mountain Research Initiative EDWWG (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change, 5*, 424–430.

Ordonez, A., & Williams, J. W. (2013). Climatic and biotic velocities for woody taxa distributions over the last 16 000 years in eastern North America. *Ecology Letters, 16*, 773–781.

Pepin, N. C., Maeda, E. E., & Williams, R. (2016). Use of remotely sensed land surface temperature as a proxy for air temperatures at high elevations: Findings from a 5000 m elevational transect across Kilimanjaro. *Journal of Geophysical Research: Atmospheres, 121*, 9998–10015.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution, 22*, 583–592.

Rao, C. R. (1982). Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology, 21*, 24–43.

Ray-Mukherjee, J., Nimon, K., Mukherjee, S., Morris, D. W., Slotow, R., Hamer, M., & Nakagawa, S. (2014). Using commonality analysis in multiple regressions: A tool to decompose regression effects in the face of multicollinearity. *Methods in Ecology and Evolution, 5*, 320–328.

Rehfeldt, G. E., Crookston, N. L., Warwell, M. V., & Evans, J. S. (2006). Empirical analyses of plant/climate relationships for the western United States. *International Journal of Plant Sciences, 167*, 1123–1150.

Reside, A. E., Welbergen, J. A., Phillips, B. L., Wardell-Johnson, G. W., Keppel, G., Ferrier, S., . . . VanDerWal, J. (2014). Characteristics of climate change refugia for Australian biodiversity. *Austral Ecology, 39*, 887–897.

Rodrigues, A. S., & Brooks, T. M. (2007). Shortcuts for biodiversity conservation planning: The effectiveness of surrogates. *Annual Review of Ecology, Evolution, and Systematics, 38*, 713–737.

Sayre, R., Dangermond, J., Frye, C., Vaughan, R., Aniello, P., Breyer, S., . . . Comer, P. (2014). *A new map of global ecological land units—An eco-physiographic stratification approach*. Washington, DC: Association of American Geographers.

Schmitz, O. J., Lawler, J. J., Beier, P., et al. (2015). Conserving biodiversity: Practical guidance about climate change adaptation approaches in support of land-use planning. *Natural Areas Journal, 35*, 190–203.

Scott, J. M., Davis, F. W., Mcghie, R. G., Wright, R. G., Groves, C., & Estes, J. (2001). Nature reserves: Do they capture the full range of America's biological diversity? *Ecological Applications, 11*, 999–1007.

Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters, 17*, 866–880.

Tingley, M. W., Darling, E. S., & Wilcove, D. S. (2014). Fine- and coarse-filter conservation strategies in a time of climate change. *Annals of the New York Academy of Sciences, 1322*, 92–109.

Wang, T., Campbell, E. M., O'Neill, G. A., & Aitken, S. N. (2012). Projecting future distributions of ecosystem climate niches: Uncertainties and management applications. *Forest Ecology and Management, 279*, 128–140.

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS One, 11*, e0156720.

Wang, T., Hamann, A., Spittlehouse, D. L., & Murdock, T. Q. (2012). ClimateWNA—High-resolution spatial climate data for western North America. *Journal of Applied Meteorology and Climatology, 51*, 16–29.

Xie, S.-P., Deser, C., Vecchi, G. A., Collins, M., Delworth, T. L., Hall, A., . . . Watanabe, M. (2015). Towards predictive understanding of regional climate change. *Nature Climate Change, 5*, 921–930.

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