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BIODIVERSITY REVIEW

The geography of climate change: implications for conservation biogeography

D. D. Ackerly[1]*, S. R. Loarie[2], W. K. Cornwell[1], S. B. Weiss[3], H. Hamilton[4], R. Branciforte[5] and N. J. B. Kraft[1]†

[1]*Department of Integrative Biology and Jepson Herbarium, University of California, Berkeley, CA 94720, USA,* [2]*Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, USA,* [3]*Creekside Center for Earth Observation, Menlo Park, CA 94025, USA,* [4]*Center for Applied Biodiversity Informatics, California Academy of Sciences, San Francisco, CA 94118, USA,* [5]*Bay Area Open Space Council, Berkeley, CA 94704, USA*

*Correspondence: D. D. Ackerly, Department of Integrative Biology and Jepson Herbarium, University of California, Berkeley, CA 94720, USA.
E-mail: dackerly@berkeley.edu

†Present address: N. J. B. Kraft, Biodiversity Research Centre, University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

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ABSTRACT

Aim Climate change poses significant threats to biodiversity, including impacts on species distributions, abundance and ecological interactions. At a landscape scale, these impacts, and biotic responses such as adaptation and migration, will be mediated by spatial heterogeneity in climate and climate change. We examine several aspects of the geography of climate change and their significance for biodiversity conservation.

Location California and Nevada, USA.

Methods Using current climate surfaces (PRISM) and two scenarios of future climate (A1b, 2070–2099, warmer-drier and warmer-wetter), we mapped disappearing, declining, expanding and novel climates, and the velocity and direction of climate change in California and Nevada. We also examined fine-scale spatial heterogeneity in protected areas of the San Francisco Bay Area in relation to reserve size, topographic complexity and distance from the ocean.

Results Under the two climate change scenarios, current climates across most of California and Nevada will shrink greatly in extent, and the climates of the highest peaks will disappear from this region. Expanding and novel climates are projected for the Central Valley. Current temperature isoclines are projected to move up to 4.9 km year^{-1} in flatter regions, but substantially slower in mountainous areas because of steep local topoclimate gradients. In the San Francisco Bay Area, climate diversity within currently protected areas increases with reserve size and proximity to the ocean (the latter because of strong coastal climate gradients). However, by 2100 of almost 500 protected areas (>100 ha), only eight of the largest are projected to experience temperatures within their currently observed range. Topoclimate variability will further increase the range of conditions experienced and needs to be incorporated in future analyses.

Main Conclusions Spatial heterogeneity in climate, from mesoclimate to topoclimate scales, represents an important spatial buffer in response to climate change, and merits increased attention in conservation planning.

Keywords

Climate change, climatic heterogeneity, conservation, protected area networks, spatial heterogeneity, spatial scale, topoclimate.

INTRODUCTION

It is widely recognized that climate change poses a grave threat to biodiversity, exacerbating existing threats because of land use change, fragmentation, and environmental degradation. In the past century, mean global surface temperature has increased almost 1 °C (Meehl *et al.*, 2007). The impacts of climate change are broadly detectable in many taxa, including shifts in phenology, distribution, and demography (Parmesan, 2006; Cleland *et al.*, 2007; Moritz *et al.*, 2008). In the next century, mean global temperature could increase by 4 °C or more, with an associated increase in the frequency of extreme events (heat waves, storms) and in the frequency and extent of wildfire (Meehl *et al.*, 2007; Westerling & Bryant, 2008;

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Krawchuk *et al.*, 2009). If the rate of change exceeds the pace of biological response, especially the capacity of populations to migrate or undergo adaptive evolutionary change, impacts on species distributions, community structure and ecosystem function may be profound. Enhanced conservation efforts, including expanded reserve systems, intensive management, and the more controversial idea of managed translocation, will play a critical role in efforts to reduce the impacts of climate change on biodiversity and ecosystem services (Heller & Zavaleta, 2009; Lawler *et al.*, 2010).

One of the most important tools in conservation planning with respect to climate change is the deployment of species distribution models to evaluate present and potential future species ranges in relation to climate, soils and other predictive variables (reviewed in Elith & Leathwick, 2009). These models can highlight individual species that may be at risk because of climate change, and geographic areas that may face substantial shifts in diversity and species composition (Thuiller *et al.*, 2005; Williams *et al.*, 2005; Loarie *et al.*, 2008). In some cases, models suggest that protected areas may no longer maintain populations of key species, possibly the very ones that the reserves were created to protect (Araujo *et al.*, 2004). Conversely, shrinking distributions and range shifts could create new refugia - areas where threatened species would be concentrated in the future (Loarie *et al.*, 2008).

The use of climate and species modelling to inform conservation faces (at least) two fundamental challenges. First, different species are expected to exhibit distinct, individualistic responses. Even if it were possible to accurately project climate change and to precisely model the biological responses, it is extremely difficult to analyse and integrate projections for hundreds or thousands of species and discern how this information should be used to inform current conservation strategies. The second issue is that the models are intrinsically uncertain, and the application of modelling to conservation is frequently overshadowed by the specter of uncertainty in model projections. Uncertainty arises at each step in the species modelling process, because of imperfect knowledge or modelling of current distributions and climates, mechanisms underlying species distributions, trajectories of future climate change, and the challenge of extrapolating species responses to novel climates, beyond the range of conditions used for model parameterization (Elith & Leathwick, 2009). Despite these limitations, species distribution models remain a critical tool, and they can be surprisingly effective at predicting observed range shifts, at least for mobile taxa like birds and butterflies (e.g., Kharouba *et al.*, 2009; Tingley *et al.*, 2009).

CLIMATE, CLIMATE CHANGE AND BIODIVERSITY

In this study, we take an alternative approach to explore the implications of projected climate change for biological communities and conservation biology. Rather than trying to improve or address the limitations of distribution models, we are interested in a variety of approaches to visualize and analyse present-day climate and future climate change projections, and to explore the implications of the results for conservation biology (e.g., Williams *et al.*, 2007; Wright *et al.*, 2009). Our analyses rest on two basic premises:

1. Biological impacts will be greater where the rate and/or magnitude of climate change is greater. Faster rates of climate change are increasingly likely to outpace some types of biological responses. The resulting disequilibrium between climate and ecological systems may increase the likelihood of crossing critical ecological thresholds and experiencing regime shifts (Scheffer *et al.*, 2001).

2. Impacts of climate change depend critically on the relationship between temporal change and spatial climatic heterogeneity. Fine-scale spatial heterogeneity should provide greater opportunity for migration and reassembly of communities, for several reasons. First, dispersal distances required to track changing conditions will be shorter, so dispersal limitation is less likely. Secondly, spatially heterogeneous landscapes in most cases support greater genetic and species diversity (Rosenzweig, 1995; Vellend & Geber, 2005). Greater genetic diversity increases the likelihood that appropriate adaptive variation will be available to facilitate adaptation to the new conditions. A diverse species pool will similarly provide a functionally diverse suite of taxa with disparate environmental affinities that can assemble into new and changing communities.

We examine three broad approaches to evaluate patterns of climate and climate change that are directly relevant to ecology and conservation biology: (1) Analysis of changes in the realized environment, and a new approach to quantify and map disappearing, declining, expanding, and novel climates that are projected as a result of 21st century climate change. (2) Integration of spatial and temporal climate patterns to evaluate the velocity and direction of climate change, i.e. how fast and in what direction does one have to move to offset future climate change (Loarie *et al.*, 2009)? For these two topics, we consider a spatial domain encompassing most of California as well as western Nevada. The extent of this domain is based on our interest in climate change impacts along the central California coast as well as the Sierra Nevada range. (3) Evaluation of spatial climatic heterogeneity at topo- and mesoclimate scales in the protected area network of the San Francisco Bay Area, and the possible role of reserve size and heterogeneity as a buffer in the face of climate change.

BUILDING A SPATIAL-TEMPORAL UNDERSTANDING OF CLIMATE

Spatial variability in climate can be nested into macroclimate, mesoclimate, topoclimate, and microclimate (Geiger & Aron, 2003). Macroclimate is the broad pattern of atmospheric circulation and synoptic meteorology across 100+ km scales of latitude and longitude, such as the N-S rainfall gradient along the Pacific Coast of North America. Mesoclimates are variations at 1–100 km reflecting penetration of marine air and effects of local mountain ranges. Topoclimates (0.01–1 km) are

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the effects of aspect, slope, relative elevation, and surrounding terrain on solar exposure, wind, and cold air drainage. Microclimate is the finest scale variability determined by vegetation cover and fine-scale (<10 m) surface features.

Investigating the geography of climate change requires the availability of spatially explicit values for climate parameters, such as monthly or annual temperature or precipitation. To establish climate 'norms', these data are derived from 20th century weather observations. To forecast geographic patterns of future climate change, values for comparable climate parameters are obtained from general circulation model outputs, usually downscaled to spatial resolutions finer than the coarse cell size of raw climate model data. Climate surfaces are interpolated, gridded representations of historical or future climate data that provide the basis for spatial analyses of changing climate patterns. In this study, we use the PRISM data set for the continental United States for analyses of current climate (Daly *et al.*, 2000). See the Data S1 for a discussion of climate surfaces and sources of uncertainty that may influence their application in conservation biology.

Changes in the realized environment

One of the basic challenges in understanding spatial and temporal patterns in climate is the multi-dimensional nature of climatic variation. Climate consists of numerous components (temperature, precipitation, wind, etc.), each with its own spatial and temporal signature. At a landscape scale, Jackson & Overpeck (2000) introduced the essential concept of the realized environment – the combinations of climate conditions that are realized, i.e. that exist, over a particular region at a given point in time. Analyses of climate maps invariably demonstrate that there are combinations of conditions that are missing. For example, California has areas with mean annual temperature >30 °C (the desert) and areas with total annual precipitation >3000 mm (the far north), but nowhere in California do these two conditions co-occur in space (if they did, we would expect tropical rainforest!) (Figs 1 & S1). Changes in the realized environment through time lead to potentially widespread phenomena of disappearing climates (present now but absent in the future) and novel climates (absent now and present in the future) (Saxon *et al.*, 2005; Williams *et al.*, 2007). Paleoecological research suggests that no-analog climates (combinations observed in the past that do not occur in the present) result in no-analog communities, with combinations of species living together that no long co-occur (Williams *et al.*, 2001). Thus, the projection of widespread novel climates in the future, relative to those that occur in today's climate space, raises the possibility of rapid realignments of communities with associated novel ecological interactions.

Our California–Nevada domain includes all or part of twelve of the WWF ecoregions of North America (Olson *et al.*, 2001) (Fig. 1a). A plot of mean annual temperature versus total annual precipitation for this region (the realized environment) illustrates a general negative relationship, from cool, wet regions in the northwest to the hot, dry deserts (Figs 1b & S1). Note that for the analyses presented here, we use $\log_{10}$ transformed precipitation because of the highly skewed distribution of values in California and the biological importance of relative changes in water availability (i.e., a change from 100 to 200 mm has a much larger biological impact than 1100 to 1200 mm). Maps of mean annual temperature, seasonality of temperature (sd of monthly means), total annual precipitation, and the seasonality of precipitation (coefficient of variation of untransformed monthly values) reveal the broad patterns of California and Great Basin climate, including the maritime zone near the coast with very low temperature seasonality, the mediterranean-type climate west of the Sierra Nevada with high rainfall seasonality, and the shift to continental-type climates east of the Sierra Nevada with greater summer rainfall (Fig. S1).

For analyses of climate change, we started with a set of 16 downscaled general circulation models (GCMs) projecting late 21st century climate (2070–2099) under the A1b development and greenhouse gas (GHG) emission scenario (Maurer *et al.*, 2007). Current trajectories of GHG emissions are higher than those considered in the A1b scenario (Raupach *et al.*, 2007), so the results presented here represent a conservative estimate of climate change. The 16 models project temperature increases

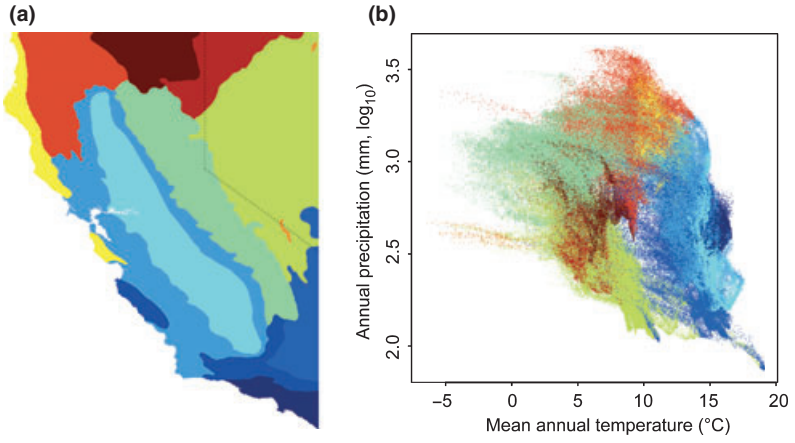

Figure 1 Spatial domain and climate space for portions of California and Nevada used for analysis in this study. (a) WWF ecoregions. (b) Mean annual temperature versus total annual precipitation ($\log_{10}$ transformed) over this domain, from PRISM historical norms (1971–2000). Colours correspond to ecoregions.

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of 2.5–3.6 °C over this century, averaged across our domain (Fig. S2). In contrast, the models produce a wide range of projections for precipitation, with changes averaged over the domain from −140 to +272 mm (−22% to +42%) (Fig. S3). Given this range of projections, the average scenario for future precipitation change is close to zero. For the analyses presented here, we selected two of the 16 models to represent a 'warmer-drier' and a 'warmer-wetter' future (Fig. S4). The drier scenario was that produced by GFDL_CM2_1.1, with mean change in precipitation of −119 mm (−18%), and close to average temperature change (+3.3 °C); the wetter scenario was from CCCMA_CGCM3_1.1, with mean change of +81 mm (12%) for precipitation, and slightly lower temperature change (+2.6 °C). Many climate change impacts studies in California also use the NCAR PCM model, which projects moderate drying (−24 mm).

Climate availability – histograms

Univariate histograms reveal bimodal distributions of temperature for the CA-NV domain, corresponding to the broad extent of cooler climates in the Great Basin and warmer climates in the Central Valley and coastal California (Fig. 2). Under both the warmer-drier and warmer-wetter scenarios, temperature increases shift these peaks 2–3 °C higher, resulting in a large increase in area under both the intermediate and high temperatures. Precipitation values ($\log_{10}$ transformed) are more or less normally distributed and the changes under both the drier and wetter scenarios represent small shifts at the extremes, and modest changes in the relative area occupied by drier and wetter climates, respectively.

Historical variability and the scaling of temperature and precipitation

While univariate histograms are a useful starting point, they fail to capture the multidimensional structure of the realized environment. Bivariate and higher dimensional analyses may use measures of summer versus winter temperature and precipitation, or temperature and precipitation means and seasonality. One of the challenges of developing integrated measures of climate change is to scale the changes projected in different climate components relative to one another. In other words, what should be considered 'equivalent' scales for axes of temperature versus precipitation, or other factors? We have modified the approach of Williams *et al.* (2007), using measures of historical, interannual variability in climate (for the period used to calculate climate norms, 1971–2000), to standardize projected future changes. This provides measures of change in each variable that can be expressed in units of

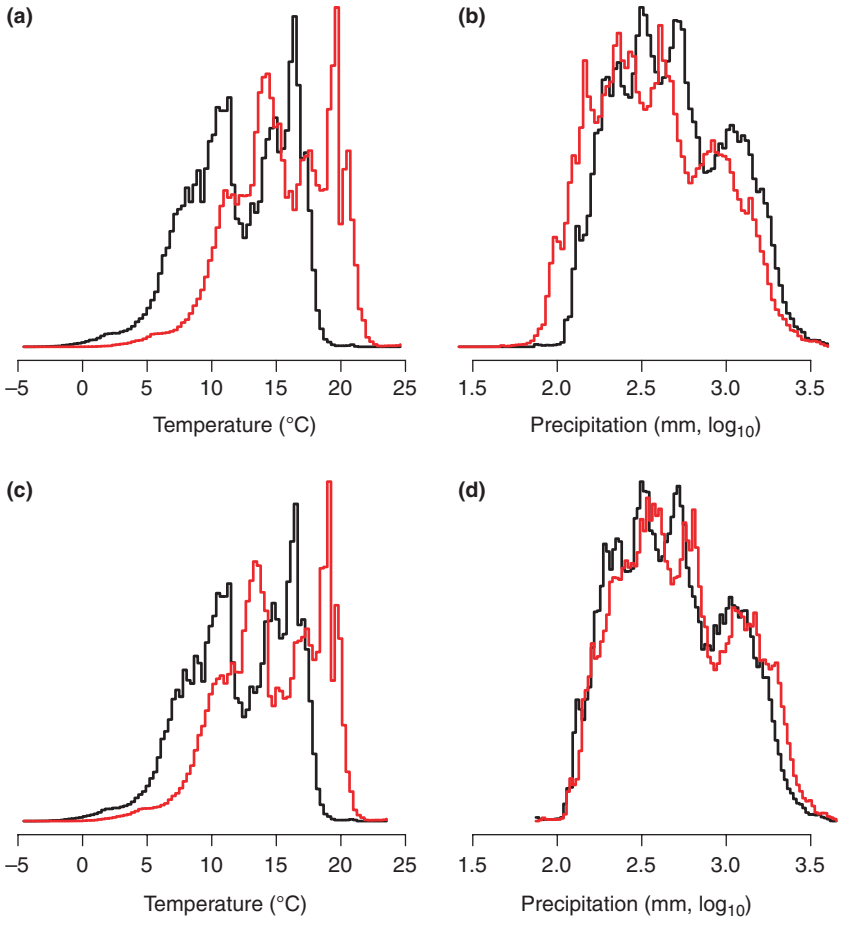

Figure 2 Histograms of climate availability for temperature (a, c) and precipitation (b, d). (a, b) warmer-drier scenario (GFDL_CM2, 2070–2099); (c, d) warmer-wetter scenario (CCCMA_CGCM3, 2070–2099). Height of the line at each point corresponds to the proportion of the area in our domain (Fig. 1) with the corresponding temperature or precipitation level in the present (black) or future (red).

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standard deviations of historical variability; the biological reasoning is that measures of historical variability will be related to the resilience of ecological systems in the face of future climate change. Based on the climatic distinctions among regions of contrasting biomes, Williams *et al.* (2007) proposed that differences of more than 3.22 sd (combined across several factors) represent substantially novel climates, either for measures of local change or comparing future climates to current conditions worldwide (also see Saxon *et al.*, 2005).

Disappearing, declining, expanding and novel climates

We have developed a modified and computationally less-intensive approach by constructing bivariate histograms of climate space, based on mean annual temperature and total precipitation, and calculating the change in area occupied by each combination of conditions. The bin sizes on each axis of our histograms were set to three times the mean value for historical variability calculated across our domain for each factor (see Fig. S5), resulting in 16 bins for temperature (each one spanning 1.75 °C), and 5 bins for precipitation (each spanning 0.45 log units). The total area occupied by each combination of temperature and precipitation, for our spatial domain, was calculated to create a 2-d histogram for the current climate and the warmer-drier and warmer-wetter projections (Figs S6 & S7). To evaluate climate change, we then divided the area occupied under the future projections by the area occupied under current climates, providing a measure of relative change in area occupied by each climate combination (=bin). Values of 0 represent a disappearing climate (present now, absent in the future), infinity is a novel climate (present in the future, absent now), and values >1 and <1 represent expanding and shrinking climates, respectively.

Under warmer-drier climates, novel climates are apparent both on the drier and hotter edges of the climate space (Fig. 3a). In contrast, under the warmer-wetter projection, novel climates appear only on the hotter edge (Fig. 3b). Under both scenarios, disappearing climates are predicted in the coldest areas. Areas of disappearing, shrinking, expanding and novel climate are mapped onto the current and future climate maps for the two climate projections. Under the warmer-drier model (Fig. 3c, d), disappearing climates are found in the highest peaks of the southern Sierra Nevada and the White Mountains. Most of our domain is occupied by shrinking climates, and in the future these climate conditions will persist primarily in the coastal mountains and the Sierra Nevada. On the other hand, small regions of the Central Valley, Owens Valley, Salinas Valley and other scattered pockets have expanding climates that will become widespread across the Central Valley, north coast, and Great Basin. Novel climates occur in much of the San Joaquin Valley and southern coastal plain (Los Angeles basin, near the edge of our spatial domain, see Klausmeyer & Shaw, 2009). Under the warmer-wetter scenario (Fig. 3e, f), the patterns are broadly similar, though the extent of novel climates is reduced.

The area occupied by a particular climate places a constraint on the diversity of associated taxa. In traditional analyses of species–area relationships, which examine contiguous areas, increased diversity in large areas is often due, at least in part, to increased environmental and climatic heterogeneity. In contrast, larger areas occupied by a particular suite of climate conditions offer more space but not greater climatic heterogeneity. Expanding climates will offer opportunities for increased abundance of native taxa, and immigration of new taxa from adjacent regions. Alien invasives are likely to be favoured in these regions, if they are able to disperse rapidly into favourable areas of expanding climates. In contrast, species that occupy declining and disappearing climates will face decreased abundance and increased chances of extinction. These analyses do not provide concrete forecasts for individual taxa, but may help to generate broader generalizations about communities and groups of species that are expected to decrease or increase under future climates. Conservation priorities will differ between these regions. Remnant areas of declining climates may be prioritized to protect taxa that have been negatively impacted by climate change. Areas of expanding climate may be particularly susceptible to invasive and weedy species, and require more intensive intervention to manage transitions to ecologically desirable future communities.

Climate movement – velocity, destination, and directional congruence

The patterns of shrinking and expanding climates shown earlier can also be thought of as the movement of climates across the landscape. Conditions that occur in one place today will shift gradually across the landscape. The predicted movement of populations upwards or polewards in response to climate change simply mirrors the fact that climate itself (in this case temperature) is moving in those directions. It is not quite right to say that populations will 'move to colder places' in response to warming. Rather, populations moving in response to climate change track similar conditions over time (unless limited by dispersal, biotic interactions, or other factors). In the case of temperature change, populations are expected to move towards places that are colder now but will not be in the future.

The spatial gradient of climate conditions on a landscape, coupled with the temporal trajectory of climate change, determines the direction and the velocity of movement for each component of climate. At any given point on a landscape, the velocity of climate change can be calculated as the ratio of the rate of temporal change divided by the spatial gradient for the same climate factor (°C/year ÷ °C/km = km/year, Loarie *et al.*, 2009). For example, if temperature is increasing at 0.03 °C $year^{-1}$ (3 °C per century) and the spatial gradient is 0.5 °C km^{-1}, as would occur on a mountainside, then the velocity is 0.06 km $year^{-1}$ (=60 m $year^{-1}$). In contrast, in a flat, temperate region the slope of the latitudinal temperature gradient is in the order of 0.005 °C km^{-1}, and the velocity to

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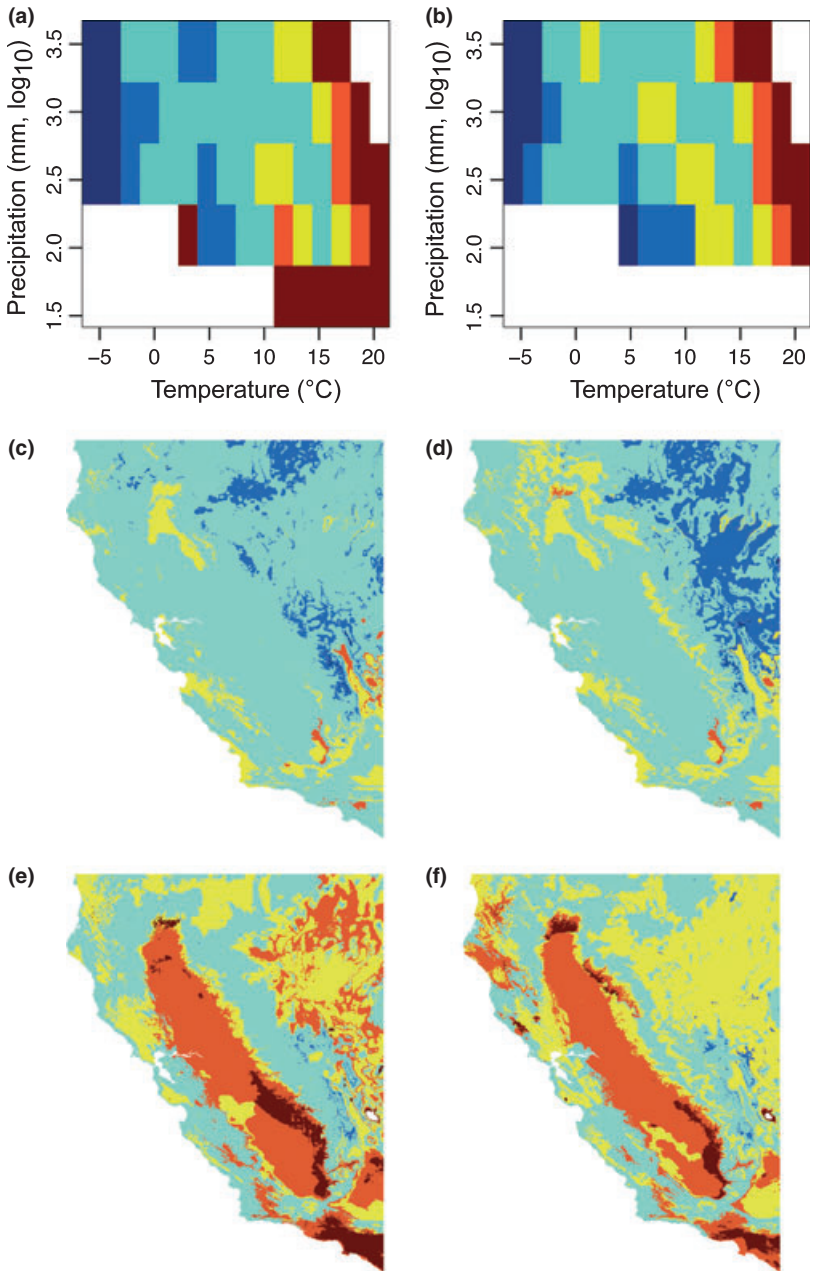

Figure 3 Histograms and maps of change in climate availability. (a, c, e) warmer-drier scenario; (b, d, f) warmer-wetter scenario. Colours represent the ratio of area available in each bin under future versus current climate: dark blue: disappearing (future = 0); medium blue: >10-fold decline; light blue: 1–10-fold decline; yellow: 1–10-fold increase; orange: >10-fold increase; dark red: novel climates (current = 0). Maps illustrate the fate of current climates (c, d) and the distribution of these climates in the future (e, f). For example, the climates that currently occupy the areas in yellow (c) are projected to expand and cover the areas shown in yellow in the future (e). In (c, d) note the very small area of disappearing climates in the high peaks of the southern Sierra Nevada and the White Mountains.

keep pace with this same rate of climate change rises to 6 km year^{-1}, rapidly outpacing dispersal rates for many organisms (Loarie *et al.*, 2009). The velocity of climate change for temperature averages 0.27 km year^{-1} and varies from 0.03 to 4.89 km year^{-1} (95% quantiles) over our spatial domain (Fig. S8a). For precipitation, velocities are generally lower, as the rate of projected change is less relative to the spatial gradients (0.01–0.92 km year^{-1} for the drier scenario and 0.00–0.46 km year^{-1} for the wetter scenario with averages of 0.08 and 0.03 respectively; Fig. S8b, c).

The direction of movement required to track shifting climate can be determined from the orientation of the spatial gradient, which will reflect topographic aspect or regional influences such as coastal climate, together with the direction of projected change in a particular climate factor. As in the example noted earlier, if temperature is increasing, then the expected migration response is towards areas that are cooler now (e.g., uphill or towards the coast). Analyses for the Owens Valley and the San Francisco Bay Area illustrate these climate-response vectors for temperature and precipitation (Fig. 4; Fig. S8d–f shows directional vectors across our entire spatial domain). For these analyses, we focus on summer temperatures (June–August mean), given the steep gradient in relation to the ocean and the general correspondence to vegetation bands from coastal forests to interior grasslands, and total rainfall. By plotting vectors of change for temperature and precipitation on the same map, one can visualize where these two aspects of climate are projected to move together, and

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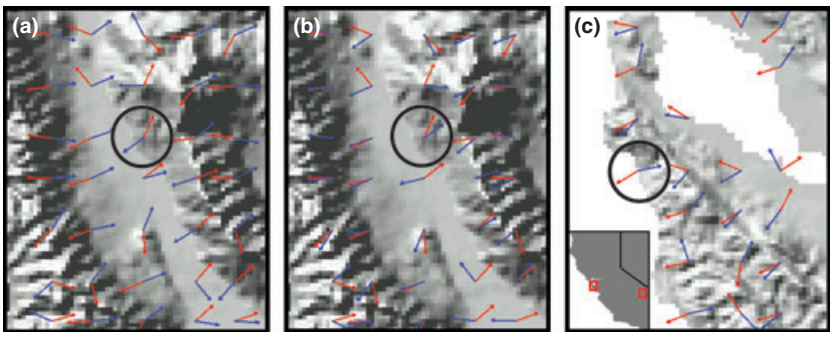

Figure 4 Vectors of movement to offset climate change (red arrows indicate direction for temperature, blue arrows for precipitation). (a, b) Owens Valley, CA under under warmer–drier (a) and warmer–wetter (b) scenarios. Circled point illustrates reversal of precipitation vector under contrasting scenarios. (c) San Francisco Peninsula; note temperature vectors oriented towards coast.

where they may be moving at right angles or even opposite directions (Fig. 4). For rainfall, the direction of the response vector reverses, depending on whether rainfall increases or decreases over time. In general, shifts towards warmer-drier climates may allow for concordant responses (Fig. 4a), because temperature decreases and rainfall often increases as one moves upslope. However, warmer-drier climates will exacerbate impacts on water balance for organisms that are not able to move.

For conservation planning, these maps of the direction of movement offer a template for expansion of existing reserves and the orientation of corridors that will facilitate movement in response to climate change. One of the striking features in the San Francisco Bay Area is that the oceanic influence leads to cooler temperatures near the coast, so westerly and downslope movement towards the coast is predicted in some places in response to increasing temperature (Fig. 4c). Further expansion of coastal reserves is of course impossible and sea level rise will encroach on coastal habitats, especially in estuaries and other flatter near-shore environments. With continued development pressure in coastal regions, climate change may pose particular threats to coastal vegetation and associated fauna.

Climate heterogeneity of protected areas

Environmental heterogeneity is a well-known factor contributing to biodiversity at a landscape scale. A recent global analysis of plant diversity found that area and topographic heterogeneity (measured as elevational range) both contributed to plant species richness, and the effect of heterogeneity was stronger in regions of high potential evapotranspiration (Kreft & Jetz, 2007). At smaller scales, plant diversity in samples of fixed size (thus removing the area effect) has been shown to increase with soil type heterogeneity (Harner & Harper, 1976). Area and heterogeneity also interact, because small areas will result in lower population sizes of each species. This effect may lead species to occupy a broader range of environments when they occur in small areas (Diamond, 1975; see Schwilk & Ackerly, 2005). Historically, conservation strategies have often focused on the 'best' exemplars of habitats, as well as targeting species of concern (Noss & Harris, 1986); such approaches will not in general lead to protection of heterogeneous and connected landscapes. A recent review identified enhanced reserve connectivity, increased reserve size and protection of a wide range of bioclimatic conditions as some of the most frequently recommended conservation strategies in response to climate change (Heller & Zavaleta, 2009), and all of these would be expected to enhance environmental heterogeneity.

We have explored the utility of ecological diversity metrics applied directly to climate maps to provide measures of the climatic diversity of protected areas. Rao's quadratic entropy (Rao, 1982), modified for a continuous distribution, is a useful measure that incorporates the evenness and degree of spread of values along a climate axis:

$$S = \frac{\sum_{i=1}^{N-1} \sum_{j=i+1}^{N} d_{i,j}}{N^2}$$

where $d_{i,j}$ is the absolute difference in climate between pixels i and j on a climate surface and N is the number of pixels (see Data S1). For the San Francisco Bay Area, we calculated values of S for summer (JJA) temperatures across each of almost 500 medium to large (100–44,000 ha), contiguous protected areas represented in the Bay Area Protected Areas Database (http://www.openspacecouncil.org/programs/index.php?program=6). As would be expected, larger reserves have higher climate diversity values ($R = 0.54$); reserves near the coast also have higher values, reflecting the steep coastal temperature gradients ($R = -0.18$; Fig. 5a) (both effects are significant in multiple regression, $P < 0.001$). To remove the size effect, residuals of S versus reserve size can be mapped, showing reserves that have higher than expected summer temperature diversity, relative to their size (Fig. 5b). Coastal reserves still have high values, but so do some smaller reserves in the interior that straddle rugged topography.

As temperature rises, many reserves may experience a complete shift such that there is no overlap between the coolest portions of the reserve in the future and the warmest portions today (based on summer temperatures at the 800 m spatial scale). In the Bay Area protected area network, under the A1b, warmer-drier scenario considered here, all but eight reserves will experience this kind of shift to entirely novel summer temperatures (Fig. 5c). In general, the degree of overlap between the coolest future temperatures and the

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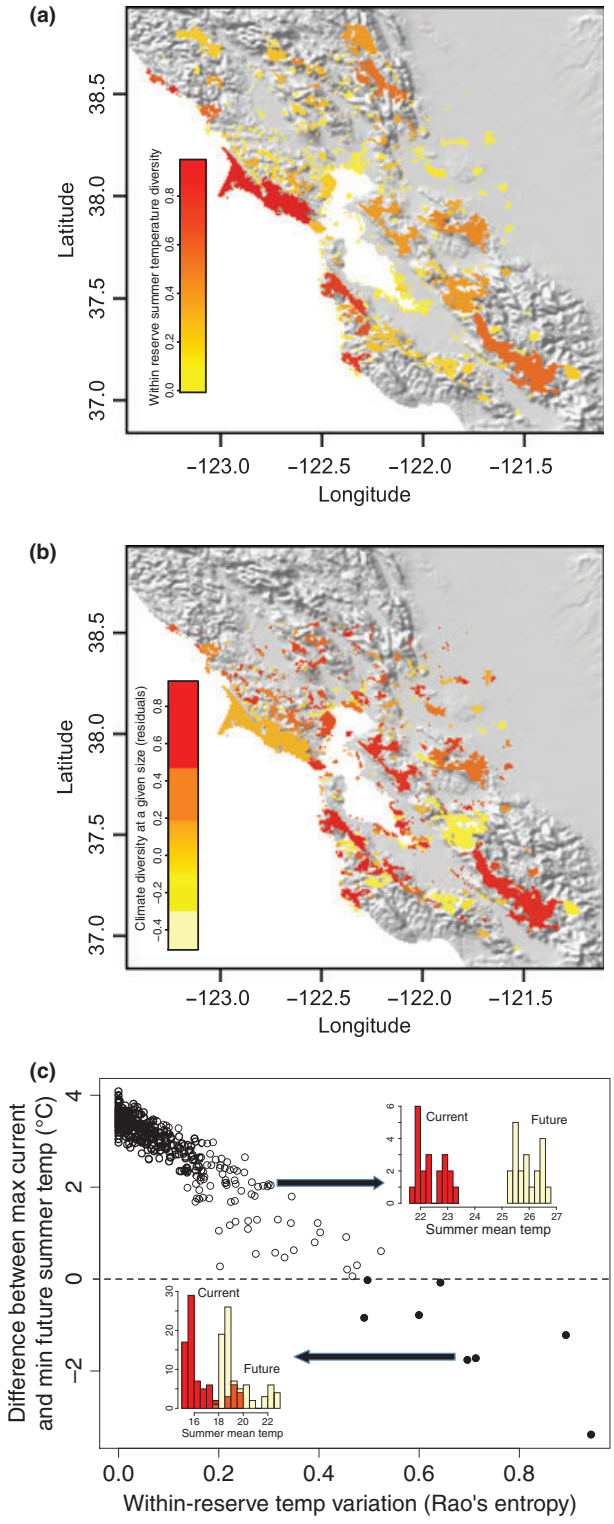
warmest current temperatures is very tightly correlated with the present climate diversity of each reserve, and also significantly higher for reserves near the coast because of the oceanic buffer on the magnitude of change ($P < 0.001$ for both factors in multiple regression).



Topography and topoclimate variation

At a finer scale (well below the 800 m pixels available in products such as PRISM and WorldClim), topoclimate diversity may provide significant spatial buffering that will modulate the local impacts of climate change (Randin *et al.*, 2009; Willis & Bhagwat, 2009). Topoclimates are fine-scale temperature gradients over tens or hundreds of metres that are driven by consistent physical processes, including cold air drainage/pooling, and insolation across slopes (Geiger & Aron, 2003). As an example, a recent empirical study in a subalpine valley at 3000 m (White Mountains, CA), illustrates the magnitude of topoclimatic gradients within a single square kilometre (Fig. 6a) (Van de Ven and Weiss, unpubl.). Temperature sensors were placed in white PVC tubes under sagebrush plants in treeless areas. The 'spaghetti' diagram of hourly temperatures, averaged from late July through early October, exhibits an 8 °C range in T_{min} at dawn, because of a strong temperature inversion with a cold valley floor and thermal belts on the slopes above. T_{max} exhibits an 8 °C range as well, tracking insolation across aspect gradients. In this area, there is no correlation between T_{min} and T_{max} ($r = -0.0024$), indicating many unique combinations of T_{max} and T_{min} within a limited area.

GIS models using slope and topographic position can project these local effects within a mesoclimate surface such as PRISM, using higher resolution digital elevation models (Van de Ven and Weiss, unpubl.). A conceptual example of this downscaling is shown in Fig. 6b for a portion of San Mateo County on the San Francisco Peninsula. The PRISM mesoclimate gradient exhibits a range of just 3 °C on this landscape, for January minimum temperatures. However, topoclimatic effects modelled at a 30-m scale add local variability on the order of 8 °C, nested within the mesoclimate. As a result, the range of topoclimates is much greater than the range of mesoclimates across this landscape (S. Weiss and R. Branciforte, unpubl.). These types of models will require local calibration, and then need to be incorporated in conservation and climate change planning.

The effects of topoclimatic gradients on distribution and abundance of organisms can be profound. In Bay Area grasslands, fine-scale topography provides resilience in the face of year-to-year climate variation, influencing emergence time of Bay Checkerspot butterflies in relation to the phenology of its host plants (Weiss *et al.*, 1988, 1993; Weiss & Weiss, 1998; Hellman *et al.*, 2004). Topoclimatic drivers

Figure 5 Variability of summer temperatures for protected areas of the San Francisco Bay Area. (a) Temperature heterogeneity across each reserve area, calculated using Rao's quadratic entropy, S (see text). (b) Residual values of S after regression on reserve size. (c) Difference between the minimum summer temperature in the future observed across each reserve (A1b, warmer–drier scenario, 2070–2099) and the maximum temperature in the present, as a function of spatial heterogeneity in temperature. Positive values indicate no overlap between current and future summer temperatures across a reserve. Insets illustrate temperature distributions for two reserves.

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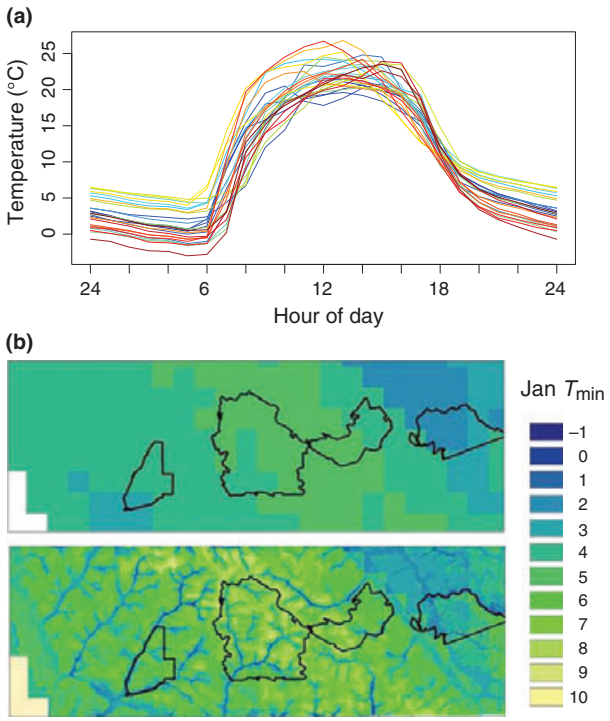

Figure 6 (a) Topoclimate in Crooked Creek Valley, White Mountains CA., as measured with a network of 26 iButton Thermochrons. Hourly temperatures were averaged over summer months. Note the 8 °C difference at 0600 h, and the different magnitude and timing of maximum temperatures. (b) Above: PRISM 800 m grid for January minimum temperatures across a portion of San Mateo County, CA. Range across the map is 3–4 °C, with spatial variability of 1–2 °C within several conservation units. Below: Topoclimatic effects on cold-air drainage (modelled at 30 m based on results in (a) nested within the PRISM gradient, effectively increasing the range within each conservation unit to 7–8 °C.

such as insolation and topographic position consistently appear in vegetation ordinations and multivariate species modelling, as well as in snowmelt models (Guisan *et al.*, 1999; Lundquist & Flint, 2006). In the White Mountains, the effective elevational difference between opposing N- and S-facing slopes is ~500 m, or ~3 °C using a standard lapse rate (Van de Ven *et al.*, 2007). Predicted responses to warming included both upward movements and local shifts across aspect, from S-slopes to N-slopes. Present distributions and observed shifts of tree populations over decades and centuries in the White Mountains confirm that these processes are ongoing (Lamarche & Mooney, 1967). In topographically complex landscapes, short-term responses to rising temperatures may manifest first as shifts of individual species and local communities from equatorial to poleward-facing slopes, or down into cold-air drainages. At these spatial scales, dispersal limitations are less likely to restrict movement, so such fine-scale heterogeneity may serve as an important spatial buffer in response to changing climate. In studies of European tree species, distribution models that incorporate fine-scale topographic heterogeneity project species persistence at a landscape scale in many cases where the coarser, mesoclimate data predicts extinction (Randin *et al.*, 2009). Paleoecological studies are also finding increased evidence that isolated 'microrefugia' in topographically protected locations have played a critical role in species persistence through unfavourable periods (Petit *et al.*, 2008).

CONCLUSIONS

Projecting the ecological consequences of climate change decades in the future is inherently difficult and yet of paramount importance. The complexity of ecological interactions, and gaps in understanding of the underlying mechanisms, pose substantial challenges (Suttle *et al.*, 2007). The appearance of novel climates is particularly important in this regard, as projections of biological response into novel portions of climate space require extrapolation beyond the conditions under which current systems can be studied and models parameterized. Where ecologists and conservation biologists are specifically interested in one or a few species or habitats of special concern, detailed research will be important to fill gaps and address these challenges. However, it is neither feasible nor in all likelihood possible to succeed in predictive modelling of ecological systems by building more complex and highly parameterized models that attempt to incorporate climate impacts on a full suite of interacting species.

In the face of these challenges, a diversity of approaches is needed and much innovative research is underway. In this study, we have highlighted a number of ways in which direct analysis and visualization of climate and climate change may be useful for ecology and conservation biology. In particular, we believe that the relationships between spatial and temporal heterogeneity at different scales are critical to understand potential impacts of climate change, and to evaluate and implement conservation strategies (Willis & Bhagwat, 2009). Fine-scale spatial heterogeneity may provide a critical buffer at a landscape and reserve scale, enhancing genetic and species diversity and reducing gene and organismal dispersal distances required to offset climate change, at least in the short run. As a general conclusion from these analyses, we advocate conservation strategies that prioritize the protection and connectivity of climatically heterogeneous landscapes and regions with declining climate extent. Such efforts are expected to buffer impacts on populations and increase the chances that rare dispersal events and local adaptive responses will occur in time to keep up with the rapidly changing climate. Research efforts must continue in parallel with conservation initiatives, to determine when and where these approaches will be successful, and when other priorities or unexpected ecological interactions may favour alternative approaches.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1 The geography of climate change: implications for conservation biogeography.

Figure S1 (a) Mean annual temperature and (b) annual temperature seasonality (standard deviation of monthly means), both derived from monthly means averaged over historical period (1971–2000). (c) Total annual precipitation (log_{10}) and (d) annual precipitation seasonality (coefficient of variation of monthly means), both derived from monthly means averaged over historical period (1971–2000). Data are from the PRISM interpolated climate database.

Figure S2 Change in (a) mean annual temperature and (b) temperature seasonality, averaged over 16 GCMs, A1b scenario, for 2070–2099. See Fig. S1a, b for baseline values.

Figure S3 Projected change in total annual precipitation for 16 GCMs, emissions scenario A1b. Mean values averaged over the domain range from −140 to 272 mm. Ranking them in order we chose the 4 and 14th models to represent drier and wetter scenarios. Drier: gfdl_cm2_1.1, −119 mm; Wetter: cccma_cgcm3_1.1, +81 mm. We also used the corresponding temperature projections for these models.

Figure S4 Change in mean annual temperature for (a) GFDL and (b) CCCMA, A1b scenario, for 2070–2099. Change in total annual precipitation for (c) GFDL (warmer-drier) and (d) CCCMA (warmer-wetter), A1b scenario, for 2070–2099. Temperature scale bars are same for Figs S2a & S4a, b.

Figure S5 Historical variability, measured as standard deviation of annual means from 1971–2000 for (a) mean annual temperature and (b) annual precipitation (log10 transformed). Mean (range) are 0.58 (0.38–1.03) for temperature and 0.15 (0.088–0.326) for precipitation.

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Figure S6 Two-dimensional histograms of climate space. (a) current; (b) warmer-drier scenario (GFDL_CM2, 2070–2099); (c) warmer-wetter scenario (CCCMA_CGCM3, 2070–2099). See text for procedure used to select bin sizes for each axis. Color intensity corresponds to area occupied by each climate combination. Due to the highly skewed distribution of areas occupied (from 1 to 24,000 km^2 for current climate), areas were log-transformed before applying the color scheme.

Figure S7 Maps of mean annual temperature and total annual precipitation (log10 transformed) for the 1971–2000 historical period (PRISM). Color breaks correspond to histogram bins in Fig. S6, illustrating geographic distribution of climates that are classified in the same bin for each variable.

Figure S8 Velocity (left) and direction (right) of climate change for temperature (a, d) and precipitation under the warmer-drier (b, e) and warmer-wetter (c, f) scenarios. Directions represent the direction of movement in space to offset projected changes in climate, and are shown using the compass wheel.

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BIOSKETCH

David Ackerly is an associate professor in the Department of Integrative Biology at University of California Berkeley. His research examines plant ecology and biogeography in the California Floristic Province, and the consequences of climate change for biodiversity and conservation.

Author contributions: S.R.L., W.K.C., S.B.W., R.B., and N.J.B.K. conducted analyses, S.R.L., W.K.C., S.B.W., and H.H. contributed text and D.D.A. led the writing.

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