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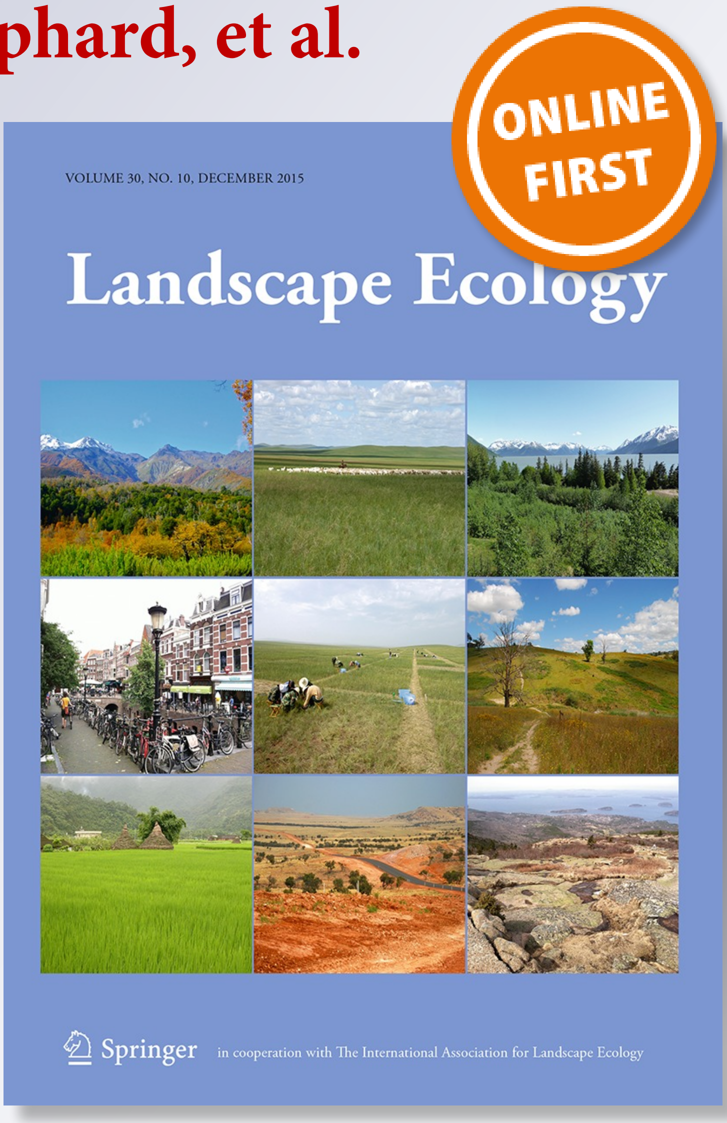

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RESEARCH ARTICLE

High and dry: high elevations disproportionately exposed to regional climate change in Mediterranean-climate landscapes

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Abstract

Context Predicting climate-driven species' range shifts depends substantially on species' exposure to climate change. Mountain landscapes contain a wide range of topoclimates and soil characteristics that are thought to mediate range shifts and buffer species' exposure. Quantifying fine-scale patterns of exposure across mountainous terrain is a key step in understanding vulnerability of species to regional climate change.

Objectives We demonstrated a transferable, flexible approach for mapping climate change exposure in a moisture-limited, mountainous California landscape across 4 climate change projections under phase 5 of the Coupled Model Intercomparison Project (CMIP5) for mid-(2040–2069) and end-of-century (2070–2099).

Methods We produced a 149-year dataset (1951–2099) of modeled climatic water deficit (CWD), which

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is strongly associated with plant distributions, at 30-m resolution to map climate change exposure in the Tehachapi Mountains, California, USA. We defined climate change exposure in terms of departure from the 1951–1980 mean and historical range of variability in CWD in individual years and 3-year moving windows.

Results Climate change exposure was generally greatest at high elevations across all future projections, though we encountered moderate topographic buffering on poleward-facing slopes. Historically dry lowlands demonstrated the least exposure to climate change.

Conclusions In moisture-limited, Mediterranean-climate landscapes, high elevations may experience the greatest exposure to climate change in the 21st century. High elevation species may thus be especially vulnerable to continued climate change as habitats shrink and historically energy-limited locations become increasingly moisture-limited in the future.

Keywords Climate change · Microenvironments · Range shifts · Climatic water deficit · Microrefugia · Topographic buffering

Introduction

Biogeographers and landscape ecologists are increasingly focusing attention on the role of local topoclimates and microclimates (hereafter referred to as "microenvironments") in mediating species' extinction risks and range shifts in response to climate change (Potter et al. 2013; Hannah et al. 2014). Mountainous topography encompasses a wide variety of microenvironments that may buffer species' exposure to climate change, allowing local retention or redistribution of species by reducing climate change velocities and providing stepping-stone habitat connectivity (Loarie et al. 2009; Ackerly et al. 2010; Scherrer and Körner 2011; De Frenne et al. 2013; Lenoir et al. 2013; Hannah et al. 2014); both of these factors may be particularly important for slowly dispersing species (Schloss et al. 2012; Zhu et al. 2012; Corlett and Westcott 2013). Methods are being developed to identify and map the distribution of microenvironments across landscapes (Ashcroft et al. 2012; Dingman et al. 2013), with the goal of using this fine-scale information to improve species distribution models (SDMs) (Franklin et al. 2013) and conservation planning under climate change (Anderson et al. 2014; Keppel et al. 2015).

The vulnerability of species to climate change is a product of their exposure and sensitivity (Williams et al. 2008). Although sensitivity is species-specific, climate exposure (hereafter, "exposure") is largely a function of local climate and can thus be projected into the future using downscaled outputs from general circulation models (GCMs). Spatial variation in the magnitude and pace of exposure can be attributed to fine-scale variation in surface energy balance, hydrology, soil characteristics and vegetation structure, all of which are thought to produce *microrefugia*, which are often defined as regionally unique microenvironments that support isolated populations of species outside their main distributions (Rull 2009; Dobrowski 2011). Microrefugia is a term taken from paleoecology, where it is primarily used to describe survival of species through glacial cycles (Bennett et al. 1991; Tzedakis et al. 2002; McLachlan et al. 2005; Stewart et al. 2010; Gavin et al. 2014; Patsiou et al. 2014). Whether the concept is useful in the context of species vulnerability to modern climate change is a topic of ongoing research and discussion (Hannah et al. 2014). For isolated populations to persist through periods of rapid climate change, the microenvironments they inhabit must be somewhat climatically decoupled from regional climate for those climate factors that limit the species' distribution (Dobrowski 2011; Hylander et al. 2015).

Conceptually, climate change at a given site constitutes a change in the probability distributions of climate variables with associated changes in descriptors of those distributions (e.g., the mean and standard deviation of the normal distribution) (Katz and Brown 1992). Changes in extremes can be particularly influential in natural systems (Easterling et al. 2000) and may be masked by analyses focused on changes in long-term means (Polade et al. 2014). Here we present an approach for quantifying the magnitude of exposure at a given site along two main axes representing change in mean annual climate and in frequency of climate extremes relative to the historical range of variability (HRV, Landres et al. 1999; Maher et al. in review) in a historical reference period (Fig. 1). Exposure has been broadly defined as

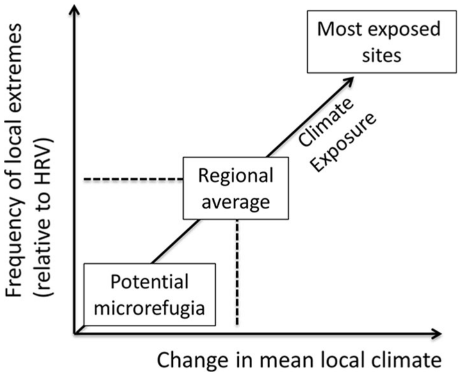

Fig. 1 Conceptual diagram of potential microrefugia in terms of climate change exposure, which is a function of both changes in mean climate and frequency of extremes relative to historical climate. The exposure of a given site is determined by its position along these two main axes

encompassing both the rate and magnitude of climate change (Dawson et al. 2011) and combined changes in both mean climate and frequency of extreme events have been previously used to assess exposure (Williams et al. 2007; Beaumont et al. 2011; Benito-Garzon et al. 2014). In mountainous regions we would expect sites to vary considerably in the rate of change in both means and extremes relative to the regional trend. Ignoring dispersal limitations, microrefugia would arguably be associated with those sites that show the least change from historical conditions (i.e., fall as near to the origin of these two axes as possible) and are thus least coupled to regional climate trends. Vulnerability of individual species will ultimately depend on their sensitivity to changes in mean and/or extreme conditions.

We applied our approach and concept of exposure to a biologically diverse mountainous study region in southern California. Because we were especially interested in plant distributions, we modeled and analyzed fine-scale changes in climatic water deficit (CWD), a bioclimatic variable that exerts strong, topographically-driven controls on plant distributions in Mediterranean-climate landscapes of California and elsewhere (Stephenson 1998; Lutz et al. 2010). We focused solely on CWD because it integrates interactions among temperature, precipitation and soil properties, all of which play a strong role in determining species distributions. Our research questions were: (1) How is CWD projected to change across a rugged landscape under mid-century and end-of-century climate projections in comparison to historical conditions? (2) How will rates of climate change exposure vary across the landscape as a function of local microenvironments?

Methods

Study area

Our study area was located in the western Tehachapi Mountains, California, USA (34°58′N, 118°35′W). This area, which is the site of ongoing research to measure and model microclimates and plant establishment (Davis and Sweet 2012), is characterized by rugged topography and steep climate gradients, providing a suitable case study of local variation in climate and projected exposure. The area is mostly private land owned and managed by the Tejon Ranch Company for cattle ranching, hunting, agriculture and rare species conservation. Our climate grids and study area covered a rectangular subregion of Tejon Ranch and some adjacent areas to the northeast, spanning approximately 33,000 ha and steep elevational gradients (370–2364 m) (Fig. 2). The climate is Mediterranean, with hot, dry summers and cool, wet winters. Mean annual precipitation for the period 1896–2010 varied from around 250 mm in the driest, low elevation portions of the area to over 500 mm at the highest elevations. At elevations above roughly 1500–1600 m, precipitation regimes are historically snow-dominated (Western Regional Climate Center 2015). Our focal climate indicator (CWD) varies widely across the landscape, mainly as a result of topographically controlled variation in solar radiation, temperature and precipitation but also due to differences in soil water holding capacity (Fig. 3). At low elevations, soils are granite-derived, coarse-loamy thermic typic Haploxerolls with maximum depths of approximately 61–122 cm (USDA 2015). High elevation sites include coarse-sandy loams derived from schist and classified as mesic Pachic Haploxerolls, as well as granite-derived medium- and coarse-sandy loams classified as mesic Haploxerolls. Maximum soil depths at high elevations are approximately 127–229 cm (USDA 2015). The topographically varied landscape supports diverse vegetation cover ranging from arid grasslands and shrublands to deciduous

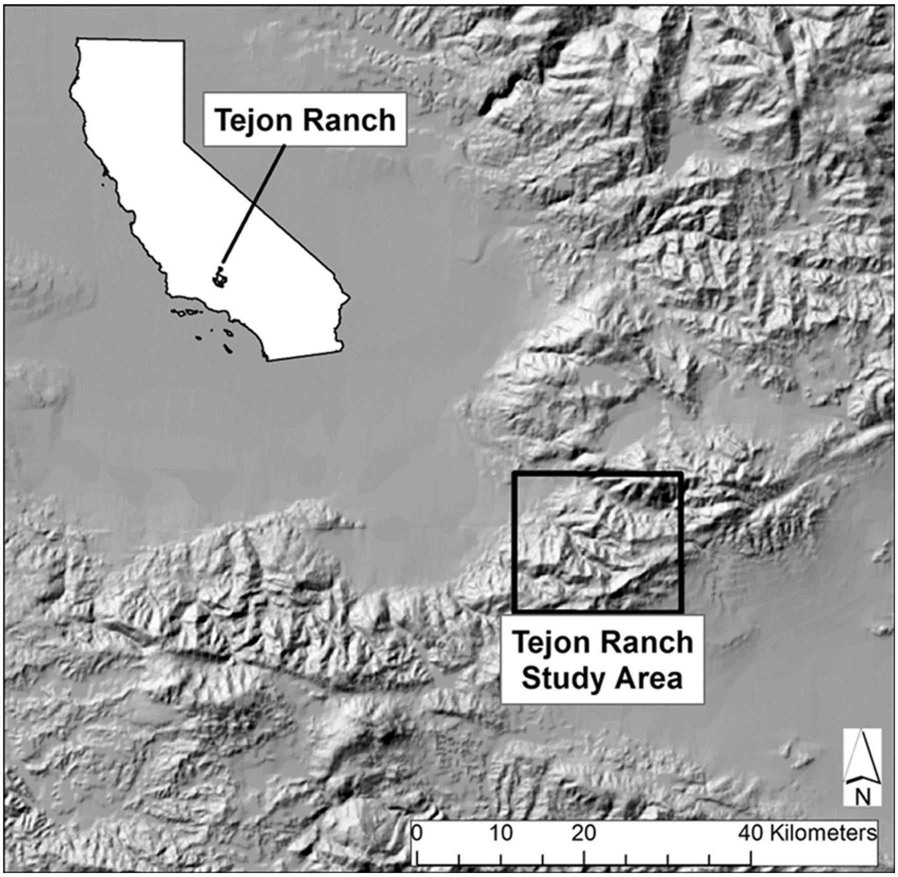

Fig. 2 *Study site*. Tejon Ranch is located in the Tehachapi Mountains, California, USA, near the southern edge of the San Joaquin Valley and the Sierra Nevada. Our model domain (*inset box*) covers 33,000 ha and an elevational gradient of 370–2364 m

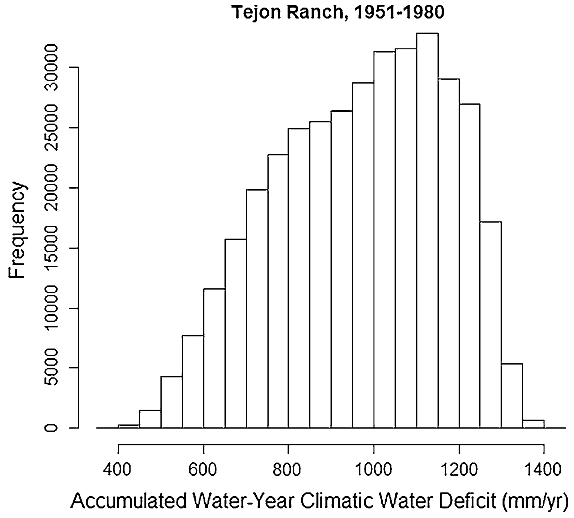

Fig. 3 Frequency distribution of accumulated water–year climatic water deficit (CWD) for Tejon Ranch expressed as cell means for 1951–1980

and evergreen oak woodlands and montane conifer forests.

Mapping historical and projected future climates

To represent historical climate conditions, parameter–elevation relationships on Independent Slopes Model (PRISM) (Daly et al. 2008) temperature and precipitation data were spatially downscaled from 800 to 30 m using Gradient-Inverse-Distance-Squared (GIDS) downscaling (Flint and Flint 2012). This method basically drapes the downscaled climate data over the landscape and has been shown either to match the coarser resolution gridded climate or improve the match to measured station data for both precipitation and air temperature by incorporating local topography, adiabatic lapse rates and climatic gradients (Flint and Flint 2012). A validation exercise was performed to provide evidence of the local skill in the downscaling for our site by comparing downscaled climate to weather station data collected at our study sites for 2012–2013 that were not used in downscaling. Correlation (r) of observed with modeled monthly averages of daily maximum air temperatures in 2013 was 0.99 (mean absolute error (MAE) = 1.73 °C) for foothill stations and 0.95 (MAE = 1.66 °C for montane stations. Correlation for minimum air temperatures was 0.97 (MAE = 1.51 °C) and 0.97 (MAE = 1.97 °C) for foothill and montane stations (3 of each), respectively, in 2013. Very similar results were obtained for 2012. Interpolated precipitation values were not as reliable. At foothill stations, correlation with monthly precipitation was 0.85 (MAE = 16 mm) in 2012 and 0.77 (MAE = 14.4 mm) in 2013. At montane stations, correlation was 0.94 (MAE = 6 mm) in 2012 and 0.84 (MAE = 6 mm) in 2013.

We analyzed 4 future projections that bracketed a reasonable range of climate futures for the Tehachapi landscape (Table 1). Due to computational constraints, we downscaled a strategic subset of Coupled Model Intercomparison Project Phase 5 (CMIP5) climate projections as part of our larger study (Davis and Sweet 2012). We chose projections using a clustering analysis that plotted future projections along two axes and directions of climate change (temperature and precipitation), placing projections in one of four quadrants (hot-dry, cool-dry, hot-wet and cool-wet) for our study area (Weiss et al. in review). We then reduced this set to nine projections that bracketed the range of climate projections across the four quadrants, which included three RCP 8.5, one RCP 6.0, two RCP 4.5 and three RCP 2.6 projections. For our study, we only considered RCP 8.5 (business-as-usual emissions for the 21st century) and 4.5 (stabilizing emissions by mid-21st century) because (1) RCP 6.0 futures are bracketed by RCP 8.5 and 4.5 projections and (2) RCP 2.6 projections are overly optimistic relative to current emissions trajectories in their requirement for declining rather than stabilizing radiative forcing by 2100 (Van Vuuren et al. 2007). The RCP 4.5 subset included the Model for Interdisciplinary Research on Climate (MIROC) and the Max Planck Institute Earth System Model (MPI). We reduced the three RCP 8.5 model subset to the Community Climate System Model v4 (CCSM4) and MIROC, excluding the intermediate model, the Flexible Global Ocean–Atmosphere-Land System Model (FGOALS), in order to use an equal number of RCP 8.5 and 4.5 projections in this study. We did not consider projections of negative temperature change due to their unrealistic nature, so we instead selected projections that were relatively cooler than the RCP 8.5 projections. We calculated the average changes projected for our study area using each model (Table 1) to verify that local projections for Tejon Ranch covered our four target climate scenarios (hot-dry, cool-dry, hot-wet and cool-wet).

Future projections were downscaled using the method of constructed analogues with bias correction and GIDS interpolation (Flint and Flint 2012). In our study area, downscaled CCSM4 and MPI models project relatively small increases in precipitation when comparing 1951–1980 to end-of-21st-century (2070–2099) levels, whereas MIROC predicts considerable decreases over the same time frame (Flint and Flint 2014). Air temperatures are projected to increase ~1.9 to 4.6 °C across the four models (Table 1). We acknowledge, however, that these 30-year mean climate descriptions potentially mask changes in temporal frequency of weather events,

Table 1 CMIP5 models used for analysis and projected climate change between baseline (1951–1980) and end-of-century (2070–2099) at Tejon Ranch

GCM	RCP	July tmax (°C)	Jan tmin (°C)	WY precip (mm)	WY cwd (mm)
Max Planck Institute Earth System Model (MPI)	4.5	1.94	1.98	24.38	92.58
Model for Interdisciplinary Research on Climate (MIROC)	4.5	2.60	1.94	−67.64	156.54
Community Climate System Model (CCSM4)	8.5	4.07	4.02	14.87	148.82
Model for Interdisciplinary Research on Climate	8.5	4.63	4.61	−111.2	244.79

WY water–year (Oct 1–Sep 30), *cwd* climatic water deficit particularly prolonged droughts and large storms (Polade et al. 2014; Berg and Hall 2015).

Modeling CWD

Mapping exposure requires accurate representation of microenvironments at biologically appropriate scales (Franklin et al. 2013; Potter et al. 2013). We produced a 149-year (1951–2099), 30-m spatial resolution dataset of annual water–year (Oct 1–Sep 30) accumulated CWD using the Basin Characterization Model (BCM). The BCM is a distributed-parameter, deterministic water balance model used to estimate potential recharge on a monthly time step (Flint et al. 2004, 2013). The model accounted for variation in climatic and edaphic conditions, integrating spatial data on precipitation amount, timing and storage, minimum and maximum air temperature, relative humidity, radiation (net short and longwave), soil–water holding capacity and vegetative cover. The BCM was calibrated and validated with 68 and 91 California watersheds, respectively, to ensure the model was regionally robust (Flint et al. 2013). Soil information was obtained from SSURGO soil databases (NRCS 2006). These climate grids were spatially downscaled using GIDS methodology applied to local elevational gradients in a multi-step process from 12 to 4 km to 30 m (Flint and Flint 2012). Potential and actual evapotranspiration were calculated using the Priestley and Taylor (1972) equation and the National Weather Service Snow-17 model (Anderson 1976). Amounts of available water below field capacity were considered as actual evapotranspiration (Flint et al. 2013). CWD was calculated as the difference between potential and actual evapotranspiration. CWD integrates precipitation, energy loading, soil water storage, and evapotranspiration and corresponds to water that would be used by plants if it were available, and relates well to the distribution of dominant plant species (Stephenson 1998). Because CWD relies heavily on temperature-induced increases in PET, CWD increases in nearly all future climate projections (Supp. Fig. 1).

Analyzing projected changes in CWD and mapping climate change exposure

To characterize the historical reference climate, we calculated mean annual accumulated water–year CWD (CWD_{WY}) for the period 1951–1980 for each 30-m grid cell (Fig. 3). We used the period of 1951–1980 as our historical baseline due to relatively stationary temperatures prior to rapid global warming in the 1980s (Fig. 1 in Hansen et al. 2006). CWD_{WY} showed no significant directional trend in our study area during this period. Prior to 1951, we lacked sufficient station data for reliable modeling of CWD across the region.

We analyzed departure from historical mean conditions (ΔCWD_{WY}) and frequency of extreme years (ΔHRV) for each 30-m cell (368,520 cells) at mid- (2040–2069) and end-of-century (2070–2099) for each CMIP5 projection. Mean CWD_{WY} increased everywhere in the landscape over the course of the 21st century, so departure from baseline mean CWD_{WY} measures the relative shift towards drier conditions of each cell. Our approach to identifying changes in extreme years was somewhat similar to that of Klausmeyer et al. (2011), who analyzed HRV in climate variables to define a "coping range" versus stressful climate conditions for landscapes in California. We used the frequency distribution of annual CWD_{WY} values within the historical reference period to define climatic extremes for each grid cell in the landscape. We expressed the departure as a percentage rather than absolute change given the more than threefold range in average CWD_{WY} across the region. We defined departure from the historical range of variability (HRV) in drought years as the number of years in each 30-year period in which CWD_{WY} exceeded approximately the 93rd percentile of the HRV (i.e., drier than all but the 2 driest years in the reference period) for each cell. We did not consider variation in extremely wet years relative to historical conditions. Because the 93 % threshold is somewhat arbitrary, we tested the sensitivity of results to cutoffs at approximately the 90th and 87th percentiles. To evaluate changes in the likelihood of multi-year droughts, which may be especially stressful to long-lived plants (Bigler et al. 2007; Vicente-Serrano et al. 2013), we also analyzed historical departure in 3-year moving windows (ΔHRV3) for the same set of GCMs, time periods and HRV thresholds. Analyses were performed using the R package "raster" (Hijmans 2015).

Arguably, sites with minimal divergence from historical climate in terms of changes in mean climate and frequency of extreme years (years outside the

HRV) offer the greatest potential as microrefugia (Fig. 1). As shown in Fig. 1, the distance of a site from the origin in this two-dimensional space represents climate exposure, which we labeled an exposure score. To facilitate comparison to percent change from mean historical climate, we re-scaled the frequency of extreme years from 0–30 to 0–100. Although previous studies used combinations of both mean climate change and frequency of extreme events to assess exposure, methods varied somewhat in terms of temporal scaling and relative contributions of means versus extremes. As such, we calculated exposure as $(\Delta \mathrm{CWD}_{\mathrm{WY}}^2 + \Delta \mathrm{HRV}^2)^{0.5}$, providing equal weight to changes in mean versus extreme climate. We mapped exposure scores across the landscape for each future projection, focusing on end-of-century projections to emphasize the requisite long-term climatic decoupling of microrefugia.

Results

Climatic water deficit

Spatial patterns of ΔHRV were similar across climate projections and time periods, but varied in magnitude (Figs. 4, 5; Table 2). Projected $\Delta \mathrm{CWD}_{\mathrm{WY}}$ changes in both means (Supp. Figs. 2, 3) and ΔHRV increased with elevation and were highest on equator-facing slopes. Under the warmest and driest projection (MIROC RCP 8.5), ΔHRV ranged from 11 to 30 out of 30 years (Fig. 4) and $\Delta \mathrm{CWD}_{\mathrm{WY}}$ increased 13–67 % by end-of-century (Supp. Fig. 2). Mitigated emissions projections (RCP 4.5) showed less divergence from the HRV and historical mean climate, particularly under the wetter MPI model (Supp. Fig. 3). Lowering the HRV thresholds slightly increased ΔHRV, particularly maximum values in RCP 4.5 projections (Table 2). Cells with the lowest ΔHRV departure rates were less sensitive to changes in thresholds across all projections (Table 2).

Values of ΔHRV3 were generally similar to ΔHRV, but with lower maxima (Table 3). Spatial patterns across the landscape were also similar, with the greatest departure rates at high elevations and lower rates on poleward (north)-facing slopes than equator-facing slopes at the same elevations. Contrary to the single-year analysis, however, rates of 3-year departures from historical climate were insensitive to more restrictive definition of the HRV (Table 3).

Mapping climate change exposure

Across all projections, exposure scores generally increased with elevation (Fig. 6, Supp. Fig. 4). However, exposure scores varied widely across the landscape and across projections, ranging from 17 for some locations under MPI to a maximum of 119 under MIROC RCP 8.5. Scatterplots of $\Delta \mathrm{CWD}_{\mathrm{WY}}$ versus ΔHRV (cf. Fig. 1) for each projection at end-of-

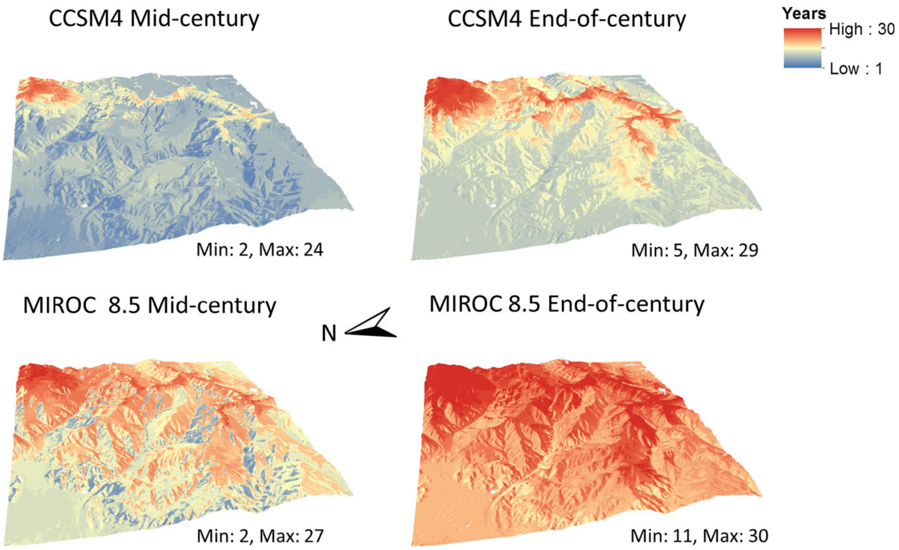

Fig. 4 Number of years of departure from the historical range of variability in terms of accumulated water–year climatic water deficit (mm/year) during mid-(2040–2069) and end-of-century (2070–2099) periods for two general circulation models (GCMs) at representative concentration pathways of 8.5: the Community Climate System Model v4 (CCSM4) and the Model for Interdisciplinary Research on Climate (MIROC)

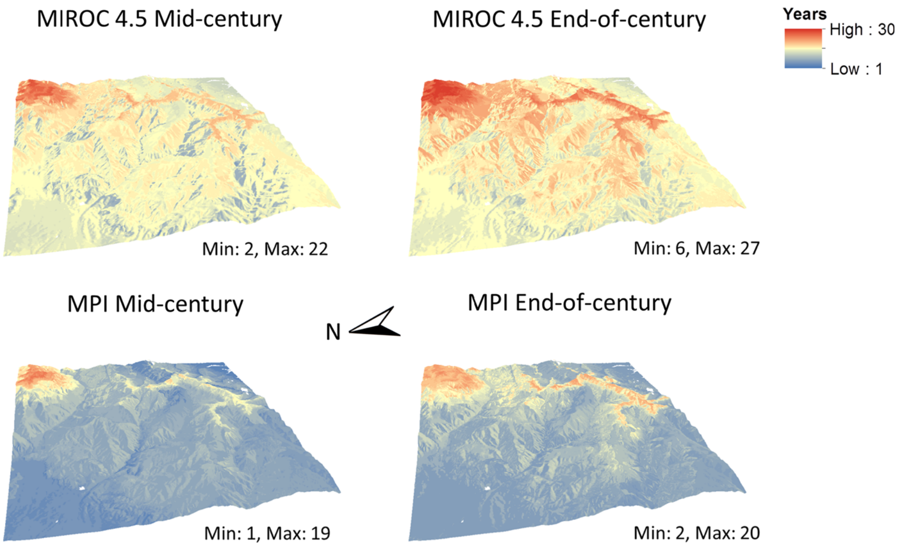

Fig. 5 Number of years of departure from the historical range of variability in terms of accumulated water–year climatic water deficit (mm/year) during mid- (2040–2069) and end-of-century (2070–2099) periods across two general circulation models (GCMs) at representative concentration pathways of 4.5: the Model for Interdisciplinary Research on Climate (MIROC) and the Max Planck Institute Earth System Model (MPI)

Table 2 Number of years (out of 30) with accumulated water–year climatic water deficit (CWD) outside the historical range of variability (presented as landscape minimum and maximum values)

GCM	93 %		90 %		87 %	
	Mid	End	Mid	End	Mid	End
CCSM4 RCP 8.5	2, 24	5, 29	2, 28	5, 30	2, 28	8, 30
MIROC RCP 8.5	2, 27	11, 30	2, 30	11, 30	2, 30	16, 30
MIROC RCP 4.5	2, 22	6, 27	2, 29	6, 30	2, 29	7, 30
MPI RCP 4.5	1, 19	2, 20	2, 27	2, 24	4, 28	4, 25

Table 3 Number of years (out of 30) with accumulated water–year climatic water deficit (CWD) outside the historical range of variability (presented as minimum and maximum landscape values) using moving 3-year averages

GCM	93 %		90 %		87 %	
	Mid	End	Mid	End	Mid	End
CCSM4 RCP 8.5	1, 23	5, 27	1, 23	5, 27	1, 23	5, 27
MIROC RCP 8.5	2, 28	9, 28	2, 28	9, 28	2, 28	9, 28
MIROC RCP 4.5	2, 22	6, 26	2, 22	6, 26	2, 22	6, 26
MPI RCP 4.5	2, 20	2, 20	2, 20	2, 20	2, 20	2, 20

century indicated that high exposure scores mainly result from high ΔHRV (Fig. 6). Topographic buffering of climate exposure occurs on poleward-facing slopes, but these areas still received relatively high exposure scores compared to flat lowlands, particularly those below 500 m (Fig. 6). Because complex topography somewhat obscures the buffering effects of poleward-facing slopes, we performed a post hoc regression tree analysis (RTA) using the R package "tree" (Ripley 2015) to explore relationships among exposure, elevation and northness (calculated as sin(slope) * cos(aspect)). The RTA revealed that although elevation was the primary control on exposure, northness reduced exposure at moderate and low elevations (Supp. Fig. 5).

Discussion

Spatial patterns of climate change exposure

Large variation in CWD-based climate exposure scores suggests considerable decoupling of local sites from regional climate trends in mountain landscapes. Whether this decoupling is adequate to support microrefugia ultimately depends on widely varying species' sensitivity to changes in either or both

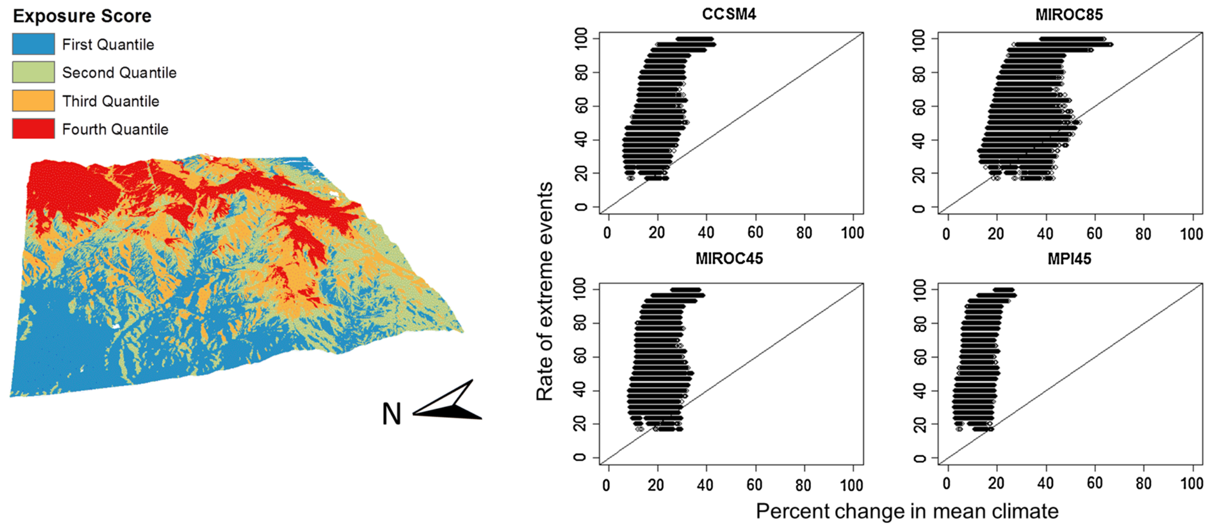

Fig. 6 Relative climate change exposure across all four climate change projections at end-of-century (2070–2099). Exposure scores were calculated for each future projection as the product of the percent change in mean climate and the rate of extreme years (departures from the HRV). Presented here are mean exposure scores across all four projections

ΔCWD_{WY} and ΔHRV. The lowest exposure scores in our landscape occurred at low elevations in sites that currently experience high CWD_{WY} and will continue to do so throughout the 21st century. Plant species currently occupying these sites (mainly annual grasses and forbs) tolerate dry conditions, though this is not to say these species are not vulnerable to other dimensions of climate change. For example, grasslands are sensitive to the timing as well as the amount of soil moisture (Hobbs et al. 2007).

We might expect microrefugia to occur in the highest (cooler and moister) portions of mountain landscapes. Our analysis suggests the opposite could be true. Those sites with historically low CWD_{WY} levels have the potential for relatively larger increases in ΔCWD_{WY} associated with warming that can affect actual evapotranspiration (AET) (Stephenson 1998). This will be especially true for historically snow-dominated sites that will receive an increasing fraction of precipitation as rain as well as shorter snowpack duration with associated increases in runoff, AET and soil evaporation (Rangwala and Miller 2012; Rangwala et al. 2013). Depending on water availability, AET will increase initially in response to warming temperatures, but will eventually level off and decline when available water is exhausted (Rosenberg et al. 1983). Exhaustion of water supplies can lead to plant mortality and vegetation type conversions (Breshears et al. 2005). Consequently, plant communities currently found at the highest elevations in moisture-limited landscapes may face shrinking habitat and limited opportunities for long-term survival under accelerated exposure (Gottfried et al. 2012).

Changes in water availability coincident with increasing temperatures at high elevations are consistent with projections for our study area. In our study region, departure from historical CWD regimes was particularly dramatic at elevations above approximately 1700 m (Figs. 4, 5). This elevation currently marked a shift from snow-dominated to rain-dominated precipitation. By end-of-century, winter temperatures are projected to raise the rain-snow transition zone above approximately 1700 m in the RCP 4.5 scenarios and above 2000 m in CCSM4 RCP 8.5, and convert the entire landscape to rain-dominated under MIROC RCP 8.5. At lower elevations, snow was historically less important or absent entirely, so changes in moisture availability in these locations are projected to be a function of changes in total precipitation. Therefore, we suspect that sites historically within the rain-snow transition zone in moisture-limited landscapes may be most exposed to climate change. Although absent from our landscape, locations that are strongly temperature-limited and that are currently far from the rain-snow transition zone (e.g., alpine or subalpine habitats) are unlikely to experience departures from historical climate as dramatic as those projected at Tejon Ranch. More generally, we would expect that both changes in overall precipitation and the position of the rain-snow transition zone will combine to influence the exposure of any given site (Tague and Peng 2013; Thorne et al. 2015).

Although high elevation areas within the changing rain-snow transition zone are likely to become increasingly "high and dry", we observed some buffering of these effects on poleward-facing slopes, which may be less exposed to climate change than other aspects and ridgetops. Systematically lower solar irradiance, lower potential evapotranspiration and longer snowpack duration compared to the rest of the landscape combined to reduce the local rate of departure from historical climate. Buffering of losses in snowpack on poleward-facing slopes may be particularly important for snow-dependent species (Curtis et al. 2014). The RTA revealed that exposure was primarily controlled by elevation in our study landscape, but with secondary, interactive effects of northness (Supp. Fig. 5). On the highest poleward-facing slopes (Fig. 6), exposure was particularly great due to warming-induced loss of historically important snow. Snow reduction accelerated increases in CWD and negated topographic buffering of northerly aspects. At lower elevations, where snow was historically uncommon or absent, poleward-facing slopes exhibited some buffering of exposure. Conversely, vegetation density and local land management history may combine to increase AET in some cases and negate the additional moisture availability on poleward-facing slopes (Guarín and Taylor 2005). Finally, absent from our discussion have been riparian areas, which were not directly defined by the BCM because, although this model calculated recharge, it did not incorporate lateral flow. Riparian areas may also reduce exposure due to accumulation of moisture, cool air and shade-providing vegetation. These topographically derived distinctions in climatic conditions represent a form of decoupling from regional climate and may produce potential microrefugia.

On the transferability of our approach

The approach we described here using departure from historical climate as a method of examining climate change exposure across landscapes is widely transferrable to other landscapes, useful for conservation planning and not subject to arbitrary decisions on the spatial extent of analysis. Although transferability will be ultimately limited by spatial (and possibly temporal) resolution of climate grids, fine spatial resolution is essential for identifying microenvironments and potential microrefugia. Increasingly fine spatial resolution has been shown to reduce rates of range shifts owing to better detection of microenvironments (Serra-Diaz et al. 2014). We recognize that downscaling from coarse GCM grids to local topoclimates introduces additional uncertainty into climate projections that remains poorly quantified (Hall 2014), but nevertheless downscaled climate projections are useful for the purpose of ecological vulnerability assessment (Franklin et al. 2013). Use of varying time windows (e.g., ΔHRV vs. ΔHRV3) provides additional flexibility in terms of temporal scaling of the interactions among climate change and species' tolerance limits. Definitions of the HRV may also be manipulated depending on the nature of the distribution of focal climate variables across years. Because our method is not tied to specific biological targets, it allows local managers to decide how local changes in climate variables interact with biological sensitivity and translate into changes in species distributions. Managers could group cells of similar rates of historical departure (e.g., 0–5 of 30 years) to analyze patch structure and configuration, if desired. In these more specific contexts, it may make sense to view landscapes through the lens of individual species (e.g., commercially valuable or keystone species); however, we believe that the generic nature of our approach boosts its transferability.

Conclusions

Considering that a common, stated objective in conservation is to protect species in the places they currently inhabit, in regions undergoing rapid climate change, microrefugia should be sites that protect the same species both now and in the future. In this vein, the allure of microrefugia is understandable. If we could only identify parts of landscapes somehow immune or resistant to climate change, we could protect and/or actively manage these sites to prevent extinctions (Keppel et al. 2012). Our analyses, however, suggest that such sites may be limited to rare localities in future landscapes. Nonetheless, we illustrate how the magnitude of climate change exposure can vary widely over short distances in heterogeneous topography and provide a means for locating areas that could experience less climate change and lower change velocities relative to regional trends. These areas may be especially valuable conservation and management targets and may play important roles in mediating range shifts and/or local persistence of species (Hannah et al. 2014; Serra-Diaz et al. 2015).

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