



Topographic, latitudinal and climatic distribution of *Pinus coulteri*: geographic range limits are not at the edge of the climate envelope

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With changing climate, many species are projected to move poleward or to higher elevations to track suitable climates. The prediction that species will move poleward assumes that geographically marginal populations are at the edge of the species' climatic range. We studied *Pinus coulteri* from the center to the northern (poleward) edge of its range, and examined three scenarios regarding the relationship between the geographic and climatic margins of a species' range. We used herbarium and iNaturalist.org records to identify *P. coulteri* sites, generated a species distribution model based on temperature, precipitation, climatic water deficit, and actual evapotranspiration, and projected suitability under future climate scenarios. In fourteen populations from the central to northern portions of the range, we conducted field studies and recorded elevation, slope and aspect (to estimate solar insolation) to examine relationships between local and regional distributions. We found that northern populations of *P. coulteri* do not occupy the cold or wet edge of the species' climatic range; mid-latitude, high elevation populations occupy the cold margin. Aspect and insolation of *P. coulteri* populations changed significantly across latitudes and elevations. Unexpectedly, northern, low-elevation stands occupy north-facing aspects and receive low insolation, while central, high-elevation stands grow on more south-facing aspects that receive higher insolation. Modeled future climate suitability is projected to be highest in the central, high elevation portion of the species range, and in low-lying coastal regions under some scenarios, with declining suitability in northern areas under most future scenarios. For *P. coulteri*, the lack of high elevation habitat combined with a major dispersal barrier may limit northward movement in response to a warming climate. Our analyses demonstrate the importance of distinguishing geographically vs. climatically marginal populations, and the importance of quantitative analysis of the realized climate space to understand species range limits.

As climate is changing around the globe (IPCC 2013), shifts in geographic range are expected to be a widespread response of plant and animal species (Hijmans and Graham 2006, Parmesan 2006, Loarie et al. 2008, Wiens et al. 2009), and these shifts have already been observed in an array of taxa (Hughes 2000, McCarty 2001). Marginal populations, occurring at the edge of a species range, are of particular interest, as it is expected that populations at the hot (trailing) edge may disappear while those at the cool (leading) edge may expand and serve as the source for propagules dispersing to new sites in response to climate change (Ackerly 2003). A crucial assumption in this simple model is that geographically marginal populations occur at the edge of a species' climatic envelope (Hickling et al. 2006, La Sorte and Thompson 2007). In the simplest case populations occupying the coldest sites, which will expand with warming, will be those closest to the poles (northernmost or southernmost populations in the Northern or Southern Hemisphere, respectively), as well as those at high elevations.

Species migration after the last glacial maximum (LGM) has been widely documented (Jackson and Weng 1999, Jackson and Overpeck 2000), and many northern hemisphere tree species (including *Pinus coulteri*, Ledig 2000) have moved north as the climate warmed. The study of marginal populations is of particular interest to understand causes of range limits and the potential responses to future climate change. Here we focus on three alternative scenarios regarding the position of the northernmost populations of a Northern Hemisphere species, in relation to the species' climatic envelope and the cold edge of the species' range (Fig. 1). Distinguishing among these scenarios is of special interest because the mechanistic explanation of the current range limit has important implications for a species' response to climate change.

The first scenario, 'climate limitation', represents a case in which the northern (poleward) populations are at the climatic edge for the species, and thus cannot tolerate climates further north (Fig. 1). In this situation, we would

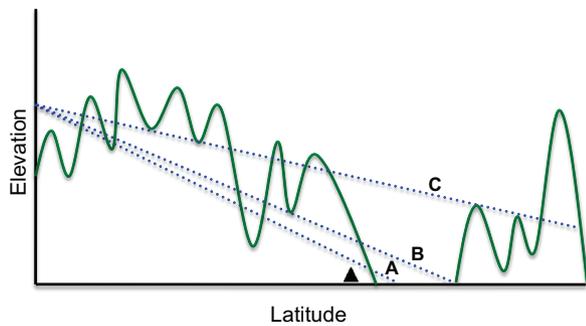


Figure 1. Three scenarios illustrating possible reasons for lack of poleward expansion past current range limit. Dotted lines represent a hypothetical isotherm of lowest temperatures, and gaps represent possible dispersal barriers. ‘▲’ represents the northernmost population. A – ‘Climate limitation’ hypothesis: northern populations are at the edge of the climatic range for the species. B – ‘Habitat availability limitation’ hypothesis: no suitable habitat is found north of the northern-most population. C – ‘Dispersal limitation’ hypothesis: presence of a dispersal barrier or dispersal lag since LGM.

expect climatic suitability to the north to improve during a period of climate warming (i.e. the current century), so the north-marginal populations would represent leading edge populations, and the species would be predicted to expand northwards. Climate limitation is the usual assumption in simple models of species distribution–climate dynamics. The second and third scenarios both involve situations in which, for different reasons, the northernmost margin of a species range is not at the cold edge of the climate envelope. The ‘habitat availability’ scenario refers to a situation in which there is a lack of appropriate habitat (for factors other than climate) further north of the marginal population, though there may be areas of suitable climate (Fig. 1). This could occur for a montane species occupying steep slopes, rocky soils, or fire-prone areas, in which there are no mountain ranges providing the required conditions beyond the north edge of the species range. Thus, the species’ cold temperature limit exists further north of the marginal population, in an area of low topographical relief that does not provide suitable habitat. Species limited by available habitat at the polar edge of their range cannot be expected to expand their ranges poleward in response to climate change. However, a species could expand its range poleward if habitat becomes available due to climate change effects on biotic interactions, fire regimes, or other processes. The final scenario is one of ‘dispersal limitation’, in which suitable habitat and climatic regions exist beyond the species’ northernmost populations. The species has not established in these suitable regions due to either dispersal lags (e.g. slow expansion since the LGM) or it has encountered a significant dispersal barrier (Fig. 1). For simplicity we present these scenarios in terms of the northern margin of a species’ range and hypothetical cold temperature climate limit, but the ideas would apply on other gradients as well.

Species that occupy mountainous regions offer valuable opportunities to test these scenarios, as upper elevation and northern range edges provide complementary information regarding climatic limits. In California, the geography of the mountains is north–south, which should, at first glance,

allow species to move poleward as the climate warms. Two factors complicate the situation in California. First, several of the mountain ranges (Sierra, Coast, Transverse, and Peninsular) reach higher elevations in central and/or southern California. Additionally, potential dispersal barriers may block movement between montane regions. *Pinus coulteri* is of particular interest in the study of marginal populations as its northern range ends abruptly at a possible major dispersal barrier (the San Francisco Bay and Delta), with extensive suitable montane habitat present north of the delta (Bay Area Open Space Council 2011). Seed dispersal by wind of *P. coulteri* is limited due to large seed and cone size and many seeds are scatter hoarded by rodents and jays in the soil, allowing for seedling establishment following fire (Johnson et al. 2003). Lower genetic variation in northern *P. coulteri* populations offers evidence of northward expansion since the LGM. Ledig (2000) hypothesized that Native Americans may have had a role in the species’ dispersal, as seeds are mentioned in trade accounts of early California tribes.

The study of topographic and microhabitat distributions at a local scale can also help to differentiate among the scenarios we propose. Plant populations frequently shift onto more exposed topographic positions (e.g. south-facing slopes in the Northern Hemisphere) or dry edaphic conditions towards the cool and moist edges of their range (along precipitation, latitude or altitude gradients; Boyko 1947, Holland and Steyn 1975). If northern marginal populations are at the climatic edge of a species’ distribution, shifts to south-facing slopes would be expected due to effects of insolation on potential evapotranspiration and water balance (Stephenson 1998).

In this study, we combine geographic and climatic analysis, detailed examination of topography within individual populations, and species distribution models (SDMs) to address the following questions: 1) do northern populations of *Pinus coulteri* occupy the climatic edge of the species distribution (i.e. do they occur at cold and/or wet limits for the species)? 2) Based on species distribution models, are suitable environments available north of the current northern range limit, and how does suitability change under projected future climates? 3) Do populations at more northerly locations occupy south-facing, higher insolation sites to offset colder temperatures and/or lower evaporative demand? 4) At a local scale, how do the sites inhabited by *P. coulteri* differ from nearby unoccupied sites, in terms of slope, aspect, and solar insolation?

The results of these analyses are used to discriminate among the alternative distributional scenarios above; we conclude that *P. coulteri* exhibits evidence of dispersal limitation at its northern range limit, and we discuss the significance of these results for potential responses to future climate change.

Material and methods

Study species and system

We examined latitudinal, elevational, and topographic distributions, in relation to regional climatic patterns,

across the California distribution of *Pinus coulteri* D. Don (Coulter pine, Pinaceae). The southern limit of this pine is located in the Sierra San Pedro Mártir range, Baja California, Mexico (~ 31°N; Critchfield and Little 1966), and its range stretches north to Black Diamond Mines Regional Preserve (BDMRP), Antioch, CA on the south shore of the San Francisco Bay Delta (37.95°N).

Pinus coulteri is part of the Closed-Cone and Four-Needle Pinyon Forest and is generally found on steep slopes in the Peninsular, Transverse and Coast Ranges. It is associated with dense chamise, mixed chaparral, and canyon live oak (Barbour et al. 2007). *Pinus coulteri* is a tree growing up to 42 m tall, and it is strongly serotinous and non-sprouting (Haller and Vivrette 2012). Populations are killed by major wildfires and regenerate synchronously from seed. In natural history circles, *P. coulteri* is best known for producing the world's heaviest pine cones (up to 5 kg fresh weight). The thick and massive scales protect seeds from fire, a frequent habitat disturbance (Johnson et al. 2003).

Current climate and distribution

We downloaded all *P. coulteri* locations available in the Consortium of California Herbaria (CCH; Consortium of California Herbaria 2014) on 4 March, 2014, and downloaded 'research grade' locations from iNaturalist.org on 17 March, 2014. We employed three criteria on these data points in order to ensure accuracy: 1) we omitted CCH occurrences with GPS error larger than 1000 m; 2) if GPS error was not included in the occurrence file, we only used specimens collected since the year 2000 which are likely to have more accurate location data; and 3) we omitted points that were clearly planted or outside of the species' known distribution. We obtained annual mean precipitation, winter minimum temperatures, summer maximum temperatures, climatic water deficit (CWD) and actual evapotranspiration (AET) (1951–1980) at a 270 m scale from the California Basin Characterization Model (BCM; Flint and Flint 2012, Flint et al. 2013). In the BCM data, monthly temperature and precipitation estimates are downscaled from the parameter-elevation regressions on independent slopes model (PRISM; Daly et al. 2002, 2008). Water balance parameters are then calculated based on estimates of potential evapotranspiration (PET) and underlying soil water holding capacity and seasonal dynamics. We averaged June, July, and August maximum temperatures and December, January, and February minimum temperatures for mean summer maximum and winter minimum temperatures, respectively. For modeling the overall species distribution, we averaged three by three cells to obtain climate averages for 800 m grids due to the variable precision of location records derived from georeferenced herbarium specimens. We obtained elevation from an 800 m digital elevation model (DEM) from the United States Geological Survey (USGS 2010). For internal consistency, we obtained all climate data from the BCM model as it includes water balance variables (CWD, AET, and PET) that are important in the semi-arid California climate (Stephenson 1998, Das et al. 2013). We did not include additional BIOCLIM layers from the WorldClim data set (Hijmans et al. 2005), which is based on an independently

derived spatial interpolation. We also did not include the southern portion of the species range in Mexico, as our climate layers do not extend beyond the California border. This omission is not expected to markedly influence the distribution modeling results at the northern, cool edge of the species range.

Species distribution model

We generated maximum entropy (MaxEnt ver. 3.3.3k) models (Phillips et al. 2004) of current and future *P. coulteri* habitat suitability, using linear, quadratic and product features, and omitting hinge and threshold features. For predictive base layers, we used 1951–1980 climate means for total annual precipitation, summer maximum temperature, winter minimum temperature, CWD and AET. The spatial domain for the models was the entire state of California, which was used for sampling of pseudoabsence values in the MaxEnt modeling. Following conventions for MaxEnt, we used the logistic output as a measure of relative suitability, based on calibration to set values with typical climatic conditions for species presence to 0.5, and we used a threshold (0.244) based on equal model sensitivity and specificity values to calculate changes in range size (Elith et al. 2011). We obtained ten future climate projections for the same factors from the Coupled Model Intercomparison Project Phase 3 (CMIP3; Meehl et al. 2007) and Phase 5 (CMIP5; Taylor et al. 2012) studies, using a multivariate approach to select models that span the range of possible futures in California. We selected only medium to high emissions scenarios (A1B and A2 from CMIP3, and rcp6.0 and rcp8.5 from CMIP5) and the end of the century (2070–2099) time span. As the future distribution modeling is not the primary object of this paper, we discuss two contrasting future scenarios: CNRM-rcp8.5 and MIROC-rcp8.5 futures, which we will refer to as CNRM and MIROC, respectively. We briefly summarize the results of other models (Table 1, Supplementary material Appendix 1, Fig A1). Future climates were downscaled onto the 30-arc second PRISM base layer, following methods in Wood et al. (2002, 2004), and processed through the BCM algorithms to provide the same temperature and hydrologic variables used for model fitting in the historical data (Thorne et al. 2012). Averaged over the Central and South West Coast regions (see maps in Baldwin et al. 2012) of California where *P. coulteri* is found, the projected changes in climate under all ten models ranged from -168.67 mm to +288.22 mm for annual precipitation, +2.75°C to +6.59°C for summer maximum temperature, and +2.60°C to +4.61°C for winter minimum temperature (Table 1).

It is important to note that MaxEnt models the species' realized climate (i.e. its realized niche), not its fundamental niche (Rodda et al. 2011). For the models to have a causal interpretation, it is implicitly assumed that distributions are in equilibrium with climate and dispersal and biotic interactions are not directly incorporated (Araujo and Peterson 2012). As a result, the models will necessarily be conservative when testing hypotheses of alternative, non-climate based distribution limits, as we do here (see below). For modeling discrete range distributions, additional assumptions are required to convert suitability to presence/absence (Elith

Table 1. Historical (1951–1980) climate values and calculated change in climate and suitability values under ten future (2070–2099) scenarios. We calculated average suitability changes from all species occupancy points used in our SDM. Changes in suitability values are shown specifically for BDMRP sites ($n = 2$), the northern range limit for *P. coulteri*. Climate means are for South West and Central West coast regions (see maps in Baldwin et al. 2012), south of San Francisco Bay, which encompass this species' range. The results discussed are shown in red.

Scenario	Precipitation (mm)	CWD (mm)	AET (mm)	Summer maximum temperature (°C)	Winter minimum temperature (°C)	Suitability change (%)	BDMRP suitability change (%)
Historical	752.08	796.96	394.79	28.49	3.99	NA	NA
CCSM4-rcp8.5	+ 65.04	+ 86.76	+ 8.3	+ 3.64	+ 3.31	-25.04	-0.76
CNRM-rcp8.5	+ 279.6	+ 73.47	+ 31.79	+ 4.04	+ 4.1	-19.83	7.04
CSIRO-A1B	+ 288.22	+ 18.19	+ 60.53	+ 2.84	+ 2.72	-16.48	-17.52
FGOALS-rcp8.5	- 10.61	+ 147.82	-38.52	+ 4.56	+ 3.32	-44.68	-4.93
GFDL-A2	-144.76	+ 149.96	-39.57	+ 3.81	+ 4.1	-38.63	19.21
GISS-AOM-A1B	+ 14.06	+ 83.84	-9.81	+ 3.17	+ 2.6	-10.23	6.82
MIROC-rcp6.0	-117.11	+ 115.73	-6.35	+ 4.98	+ 3.29	-48	-34.9
MIROC-rcp8.5	-168.67	+ 182.61	-39.58	+ 6.59	+ 4.61	-58.8	-30.79
MIROC3-2-A2	-152.36	+ 155.39	-39.16	+ 5.45	+ 3.35	-63.76	-24.54
PCM-A2	+ 69.33	+ 73.97	+ 11.84	+ 2.75	+ 2.61	-20.78	4.59

et al. 2011, Liu et al. 2013). Here, we compare current and future projections from the same underlying model, either by directly examining changes in the underlying suitability surface or changes in range size based on a constant threshold value.

Within site sampling

We chose fourteen *P. coulteri* populations from the central and northern portions of the species range in central California based on prior location information and accessibility for detailed field studies (Table 2). These data permitted us to examine local-scale topographic distributions within populations in relation to climate, latitude and elevation. As we aimed to closely examine the northern range limit of this species, conducting field studies in the southern half of *P. coulteri*'s distribution was beyond the scope of our study. The sites chosen are representative of the major *P. coulteri* populations in this region (Fig. 2), and include the furthest north population of the species at BDMRP. It is unlikely that undocumented populations exist further north as *P. coulteri*'s large and distinctive cones make it famous among local plant enthusiasts. Our goal was to determine whether *P. coulteri* individuals occupied different topographic positions (slope and aspect) along its latitudinal and elevation gradient as well as compared to closely adjacent areas where the species was absent. Thus, at each field site, we sampled a total of forty points (twenty occupied by *P. coulteri* and twenty unoccupied) for detailed examination of topography between June and September 2010.

Sample points

At each site, we identified *P. coulteri* stand(s) and chose the largest stand with a road/trail passing through it for strip-transect sampling. We sampled twenty evenly spaced points along the road/trail to record microhabitat topography around the nearest *P. coulteri*. We then sampled twenty randomly located points not occupied by *P. coulteri* for comparison of topographic features. We chose unoccupied sites within an area of 2 by 2 km surrounding each *P. coulteri*

stand. We provided details of point selection methods in the Supplementary material Appendix 1.

Measurements

At every sampling point, we used a 10 m radius around a *P. coulteri* individual (i.e. occupied point) or around an unoccupied point for measurements of slope and aspect (Conventional Pocket Transit Compass, Brunton, Riverton, WY). We recorded latitude and longitude at each point with a Garmin GPSmap 60CS× (GARMIN International, Olathe, KS). To obtain a fine scale climate parameter, we estimated annual insolation following the approximations of McCune and Keon (2002), based on latitude, slope and aspect measured at each sampled point. We were unable to directly estimate climate values (temperature, CWD or AET) as these layers are estimated on a 270 m grid, which is too coarse given the local scale of our sampling.

Analysis

To characterize the climate space for the species, we compared climate occupied by all *P. coulteri* sites in our statewide dataset to the background of distribution climate values for the Central West and South West bioregions where the species occurs, as defined in the Jepson manual (Baldwin et al. 2012).

We performed statistical analyses in R ver. 3.0.2 (R Project for Statistical Computing). To account for grouping of sample points by site, we ran linear mixed effects regressions (LMERs) for the effect of latitude and species occupancy on aspect and insolation for all individual sampled points ($n = 560$), with site as a random variable. Latitude, aspect and insolation are continuous variables and species occupancy is a binomial variable. We then ran an analysis of covariance (ANCOVA) on our LMERs to examine the effect of latitude, species occupancy, and their interaction on aspect and insolation (Table 3). This provided a test for differences in local scale topography and insolation between *P. coulteri* microhabitats and their surrounding areas.

Table 2. Sampled sites with corresponding county, latitude, elevation, annual precipitation, winter minimum temperature, summer maximum temperature, slope, aspect, and annual average insolation. Highest and lowest climate values shown in red and blue, respectively. Northernmost population denoted with *.

Site	County	Latitude (°)	Elevation (m)	Annual precipitation (mm)	Winter minimum (°C)	Summer maximum (°C)	Slope (°)	Aspect (cosine of ° from North)	Insolation (MJ cm ⁻² yr ⁻¹)
Figuerro Mt	Santa Barbara	34.73	1103	76.38	3.77	28.95	19	-0.75	1.05
Pine Mt	San Louis Obispo	35.33	862	56.49	3.29	31.06	12	-0.42	0.98
Alder Peak	Monterey	35.88	1014	141.17	4.08	23.83	22	-0.54	0.97
South Coast Ridge Rd	Monterey	35.9	951	136.97	4.00	24.66	28	-0.08	0.86
China Camp, Carmel Valley	Monterey	36.29	1336	97.37	0.72	27.13	32	-0.21	0.91
Chew's Ridge	Monterey	36.31	1394	89.7	0.56	26.95	22	-0.58	0.99
Laguna Mt	Benito	36.34	1284	57.66	2.56	28.43	16	0.73	0.84
San Benito Mt	Benito	36.38	1343	51.1	2.24	27.58	18	0.13	0.88
Fremont State Park	Monterey/San Benito	36.76	830	70.46	2.83	26.42	20	0.26	0.89
Mt Hamilton	Santa Clara	37.35	1091	57.89	3.09	26.41	34	0.63	0.64
Mitchell Rock, Mt Diablo	Contra Costa	37.91	260	48.48	4.08	29.76	22	0.88	0.75
Donner Canyon, Mt Diablo	Contra Costa	37.91	282	52.07	4.63	30.00	33	0.64	0.56
Jim's Place, BDMRP*	Contra Costa	37.95	425	53.61	4.83	30.26	21	0.80	0.69
Ridge Trail, BDMRP*	Contra Costa	37.95	268	50.06	4.11	30.23	17	0.59	0.84

Results

Current climate and distribution

The current distribution of *P. coulteri* is restricted to the Coast, Transverse and Peninsular Ranges of central and southern California, USA and Baja California, Mexico (Fig. 2; Critchfield and Little 1966, Barbour et al. 2007). Northern sites are generally at lower elevation (260–425 m) than the southern sites within the species' California range (Fig. 3A). At its absolute southern range limit in the Sierra Juárez Mountains, this species is found at even higher elevations (1450–1700 m; Moran 1977). The species experiences annual precipitation of 359 to 1582 mm, CWD of 406 to 1104 mm, AET of 221 to 610 mm, summer maximum temperatures of 22.3°C to 35.2°C, and winter minimum temperatures of -4.5° to 7.8°C. (Fig. 3B–C). Populations in the Sierra de Juárez and Sierra San Pedro Mártir occupy the hottest climates (summer maximum temperature >34°C) at the dry edge of the species range (annual precipitation 382 mm; CONAGUA 2010). We found that *P. coulteri* populations at the northern (polar) geographic limit of the range are not at the climatic edge of the species for any of the variables studied here (Fig. 3, Table 2). Rather, the climatically cold-margin populations are found in central, high elevation sites (Table 2).

Species distribution model

MaxEnt provided a strong fit of current *P. coulteri* distribution to the historic climate layers, with an area under the curve (AUC) statistic of 0.950. Multivariate environmental similarity surface (MESS) maps, which examine future climates relative to the range of historical conditions (Elith et al. 2011), show only dissimilarity in winter minimum temperature values in the coastal regions of the San Francisco peninsula and the East Bay Area as well as the Los Angeles basin. With a high AUC statistic and appropriate MESS maps, we are confident that our SDMs fit the data well and can be used to examine responses to future climate change within this spatial domain. Summer maximum temperature had the strongest contribution to the model fit (25.8% contribution), followed by CWD (24.7%), AET (24.1%), precipitation (15.5%) and winter minimum temperature (9.8%). The current climate suitable for *P. coulteri* encompasses most of the Peninsular, Transverse and Coast Ranges up to San Francisco Bay, and the southern part of the Sierra Nevada (Fig. 4A). Areas of high climatic suitability occur north of the San Francisco Bay Delta, comparable to suitability south of the delta, where the northernmost *P. coulteri* populations are found (Fig. 4A inset). Note that a species distribution model provides a conservative estimate of climatic suitability if there is dispersal limitation, as the estimate of the climatic envelope is necessarily based on currently occupied habitat. Including all habitat locations that meet the climatic requirements for this species would likely expand the range of suitable climate.

Under future warming scenarios, suitability for this species is projected to decrease between 10.23% (GISS-AOM-A1B scenario) and 63.76% (MIROC3-3-A2 scenario) averaged

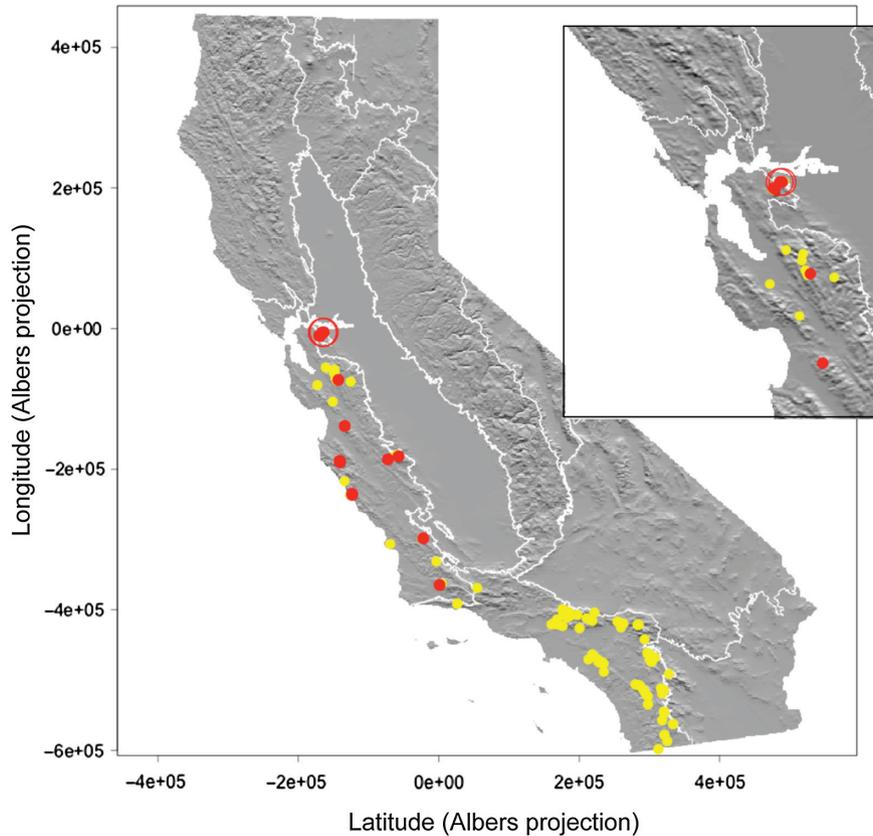


Figure 2. Shaded topographic map in Albers equal-area projection of California, USA, with all *P. coulteri* locations shown in yellow (Consortium of California Herbaria 2012, iNaturalist.org 2014) and sampled locations shown in red. Northernmost populations (BDMRP) are denoted with hollow red circles. *Pinus coulteri* locations in Baja California, Mexico, not shown. Northern portion of the species' range is enlarged and the San Francisco Bay and Delta shown in white.

across the sites where it currently occurs (Table 1). Under the CNRM model, with less extreme warming and a slight increase in rainfall, suitability decreases less and remains high at high elevations of central and southern California (Fig 4B). With greater warming (MIROC), regions of high suitability shift upslope in the Sierra Nevada (outside the species range) and towards the coast where summer temperatures are cool due to maritime climate (Fig. 4C). Under six of ten scenarios, suitability at the site of the current northernmost populations in the Bay Area is projected to decrease (Table 1, Supplementary material Appendix 1,

Table 3. Degrees of freedom (DF), sums of squares (SS), and F values from LMER results for the effect of latitude and species occupancy on aspect and insolation for all individual sampled points (n = 560), with site as a random variable. Interaction values indicate the significance of interaction between latitude and occupied/unoccupied point. P-values shown next to F values with the following notation: $p < 0.001$ ***.

Response variable	Parameter	DF	SS	F value
Aspect	occupied/unoccupied	1	0.09	14.52***
	latitude	1	17.06	23.77***
	interaction	1	5.15	14.78***
Insolation	occupied/unoccupied	1	0.04	15.236***
	latitude	1	0.63	17.64***
	interaction	1	0.29	15.66***

Fig. A1). Due to the lack of high mountains in the Bay Area, suitable regions for higher elevation colonization in response to warming are not available. Using the threshold of 0.244, suitability values were converted to binary range maps under historic and future climates. Across the entire state, range contraction exceeds expansion, and range size is projected to decrease in all but one scenario (Supplementary material Appendix 1, Table A1, Fig. A2). Under the warmer and slightly wetter CNRM model, modest range contractions occur throughout this species' distribution (Fig. 4b and Supplementary material Appendix 1, Fig. A2). Under the drier MIROC model, declines are more dramatic in the south coast, and the species is projected to shift closer to the coast in the Bay Area with slightly expanding potential distribution (Fig. 4C), leading to a dramatic decline in suitability at the northern populations situated further inland (Table 1).

Site level analyses

Northern, low elevation populations are located on north-facing slopes and the mid-range (high elevation) populations are on south-facing slopes, corresponding to lower and higher yearly insolation values, respectively (Fig. 5A). Additionally, northern stands grow on steeper slopes than mid-range stands ($p < 0.001$). Insolation is not correlated with summer maximum temperature (Fig. 5B) or winter

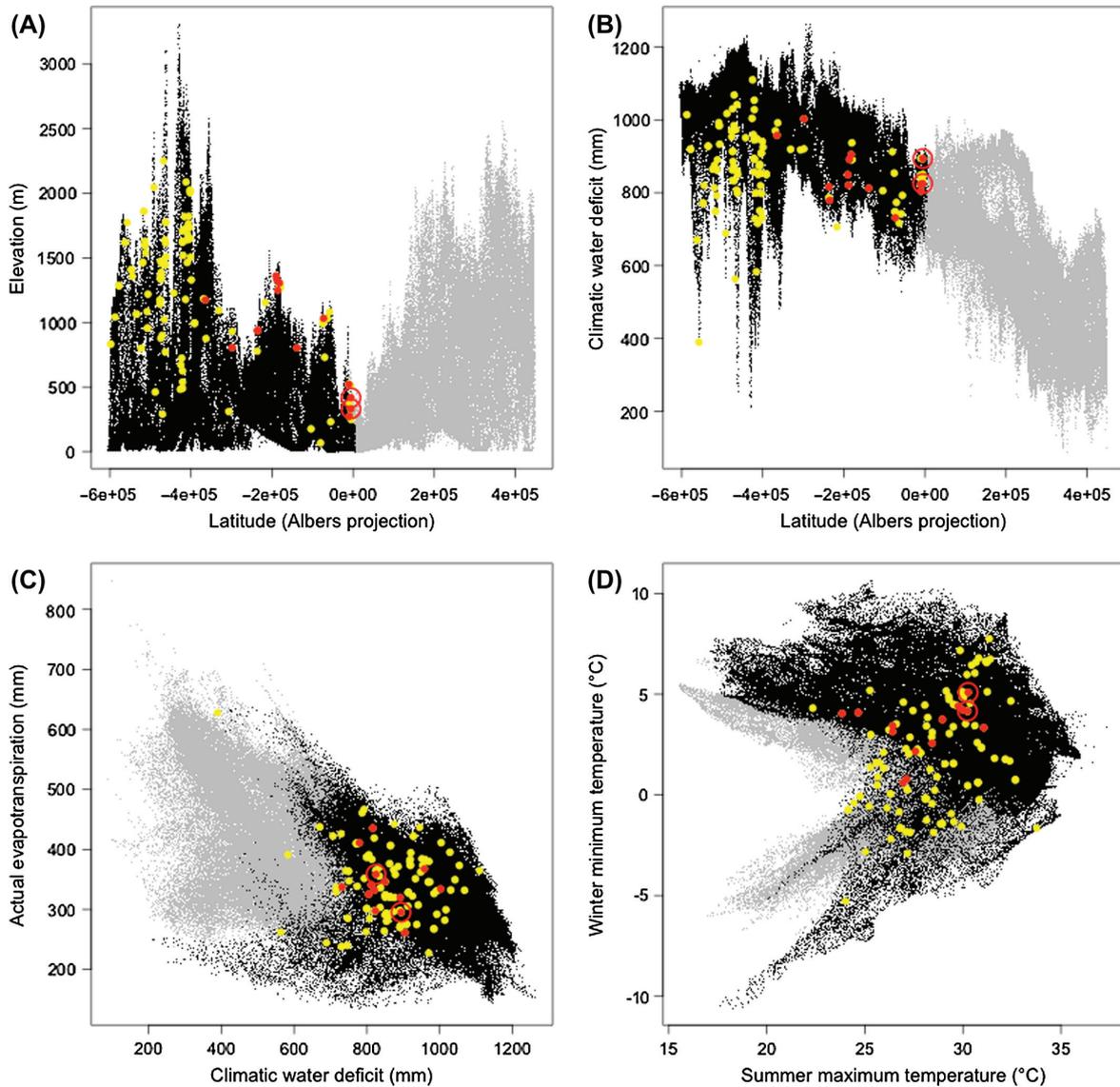


Figure 3. California Coastal Ranges and *P. coulteri* climates. Coastal Range climate north of the Bay Area shown in grey, Coastal Range climate south of the Bay Area in black, all *P. coulteri* locations in yellow ($n = 137$), and sampled sites in red ($n = 14$). The northernmost populations (BDMRP) are denoted with red circles. (A) High elevation populations are only found in southern California, and northern populations are found at the lower elevational limit for the species. (B) Southern populations experience the entire range of CWD values for the species whereas as northernmost populations experience average CWD. No populations are found at low CWD values. (C) AET and CWD values for this species are spread throughout Coastal Range values. Northernmost populations are not at the edge of AET or CWD ranges for the species. (D) *Pinus coulteri* climate is spread throughout average Coastal Range climate. Geographic range limits do not match climate limits, as northernmost populations are not at the edge of this species' climate space at neither maximum nor minimum temperatures.

minimum temperature from the regional climate maps, so there is no evidence that topographic position mediates temperature differences across the range. The full range of insolation values experienced by *P. coulteri* habitats is seen at low precipitation values, with higher insolation values observed with higher annual precipitation showing that the species shifts to south-facing slopes in wetter locations (Fig. 5C).

Occupied—unoccupied points

There is a significant ($p < 0.001$) effect of latitude and *P. coulteri* occupancy on aspect and insolation (Table 3,

Fig. 6A, B). At northern, lower elevation sites, occupied points are more north-facing and receive lower yearly insolation than unoccupied points in the immediate vicinity. We can see that this species inhabits low elevations and north-facing slopes in the northern part of its range, and higher elevations and south-facing slopes in the central portion of its range in Fig. 6A.

Discussion

We found that *P. coulteri* populations in California are unlikely to be able to expand northward with a changing climate, and

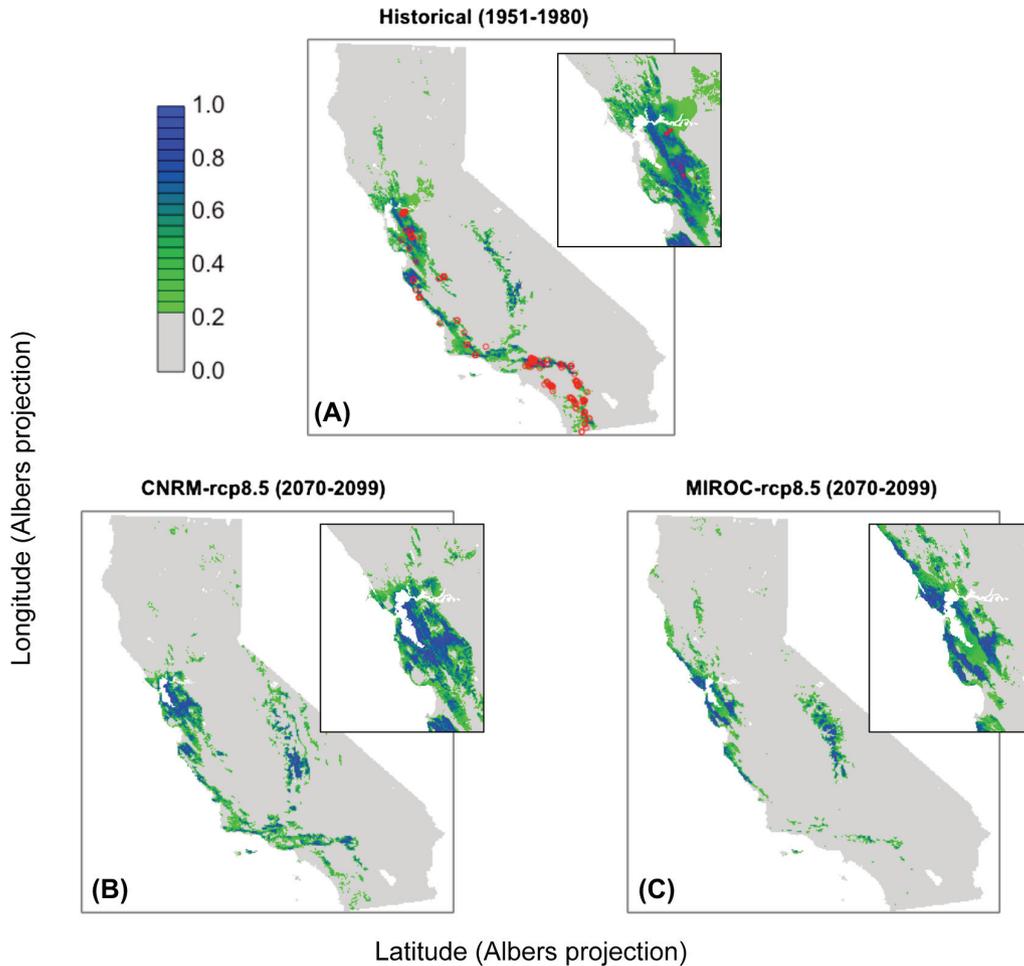


Figure 4. Current and future suitability projections from MaxEnt models with the northern portion of *P. coulteri* range enlarged. Black circles show current locations. (A) The current climate suitability model for *P. coulteri* shows suitability north and south of the San Francisco Bay Delta (i.e. species' range limit). Future climate suitability model for Coulter pine under the (B) CNRM-rcp8.5 and (C) MIROC-rcp8.5 scenarios. Suitability is projected to decline throughout all of the *P. coulteri* range. Bluer colors show areas with more suitable conditions. We selected the equal sensitivity and specificity threshold of 0.244 to eliminate low suitability values.

instead southern, higher elevation areas will be most suitable for expansion. We present three lines of evidence that suggest that future migration direction and rate for *P. coulteri* will not be a progression northward. We found that 1) northern limit populations of this species do not occupy the species' cold/wet climatic extremes; 2) current species distribution models find suitable climates north of the San Francisco Bay Delta, but suitability in the north declines under most future scenarios; 3) populations at the northern range limit are in low insolation sites and also inhabit microsites of lower insolation compared to surrounding, unoccupied sites. Collectively, this evidence suggests that the current northern limit for *P. coulteri* is not at the cold or wet climatic limit for the species, and is probably set by dispersal limitation at San Francisco Bay and Delta. This dispersal barrier would limit short-term migration responses to climate change, and the distribution model we consider here also suggests that climate suitability in northern locations will decline in the future.

Current climate and distribution

Contrary to our expectations, we observed that *P. coulteri* populations at the northern range limit are not at the edge of

the climate range for the species (Fig. 3B–D, Table 2). The northernmost populations exhibit intermediate values for all four climate parameters we examined, while low and high elevation populations further south exhibit the respective extremes. These patterns strongly suggest that the northern limit for this species is not determined by climatic limitation. This interpretation is further strengthened by our SDM (Fig. 4), which shows areas of suitable climate on the north side of San Francisco Bay and Delta. Similarly, Fig. 3 shows a nearly identical climate experienced by *P. coulteri*'s northernmost populations just north of the species' range limit. The San Francisco Bay and Delta divides the Coast Range geographically, and the comparable climates seen on either side (compare adjacent black and grey points in Fig. 3A,B) further support our hypothesis that this species is dispersal limited.

It is possible that these areas adjacent to the species' range limit are climatically suitable, but do not provide appropriate habitat (e.g. soils, fire regimes, etc.) which would correspond to our habitat limitation hypothesis. While we cannot eliminate this possibility, it seems unlikely as the terrain in the region north of the delta is similar to the areas occupied south of the delta, and there is a history of wildfire in both regions that would promote establishment and regeneration

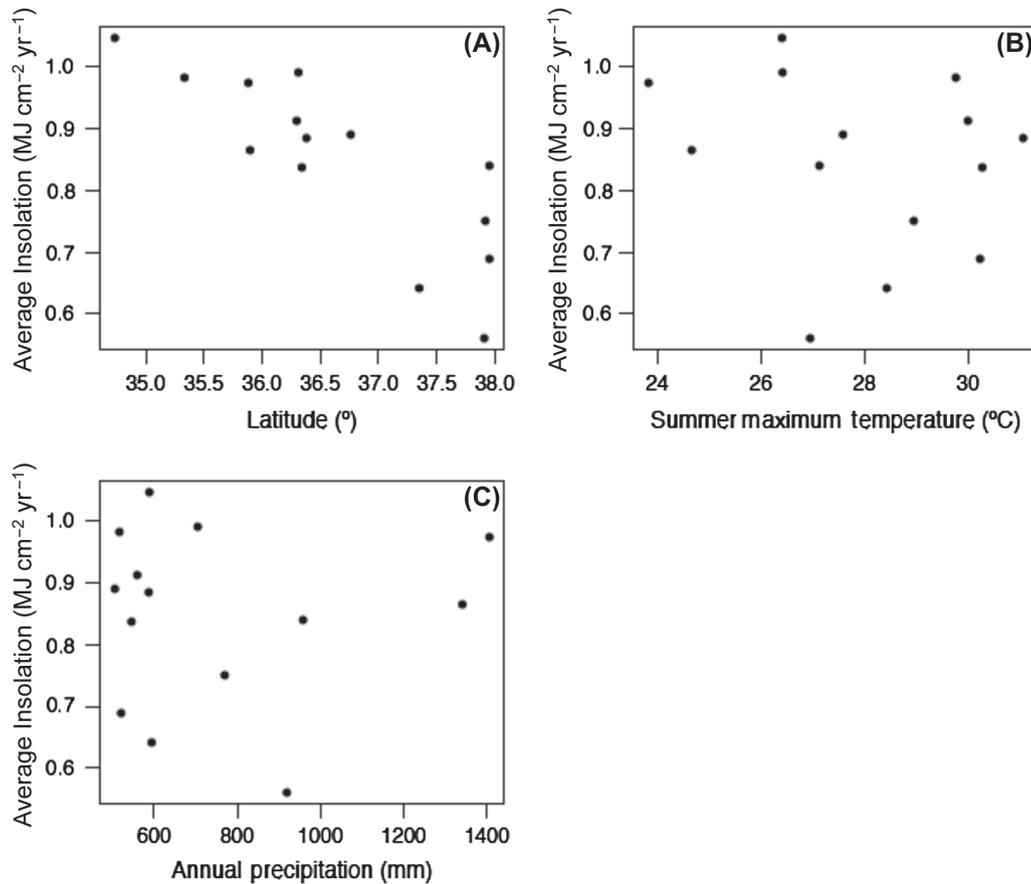


Figure 5. Insolation compared to latitude, summer maximum temperature, and annual precipitation at every site. Site means ($n = 14$) calculated from occupied points ($n = 20$ per site). (A) Northernmost populations receive less yearly insolation than southern populations. (B) Insolation is not well correlated with maximum summer temperatures. (C) A large range of insolation values is seen with low annual precipitation, and only high insolation values are seen with high annual precipitation. Northernmost sites receive low annual precipitation and insolation.

of the species. In addition, *P. coulteri* was planted in the past on Mt Tamalpais in Marin County north of the delta as part of an effort to increase forest cover in the park (California State Parks pers. comm.). More recently, these trees were removed, but their previous growth demonstrates the climatic suitability of the region. The combination of genetic evidence of northward expansion following the LGM (Ledig 2000), the existence of a significant physical barrier (the San Francisco Bay and Delta), and the apparent climatic and topographic suitability of regions further north, collectively suggest that this species northern distribution limit reflects dispersal limitation, rather than the limits of climatic suitability.

Prior studies of *P. coulteri* suggest that both dispersal limitation and drought tolerance are important factors limiting the species range. While we explored the northern range limit for this species, Minnich and Everett (2001) show that throughout its abundant distribution in southern California, *P. coulteri* is absent from several large regions that are comparable in climate and topography, again suggesting a role for dispersal limitation. Several studies show that this species is also limited by drought stress, a factor important in the central and southern portion of the range. Our climate analyses are consistent with this, as we show that regions with higher CWD values are generally unoccupied in the southern part of the range (Fig. 3B). Wright (1970) posits that the lower

elevational range limit in the San Bernardino Mountains of southern California reflects drought tolerance as well as avoidance (via relatively deep roots), together with patterns of post-fire regeneration. Similarly, Poulos et al. (2012) show that water availability is the major factor controlling tree distributions in this mountain range. Their conclusions that *P. coulteri* is a drought avoider explains why this pine is not found at low elevations in the central portion of its range.

Species distribution model

With changing California climate, there is a high interest in projecting the future range of native species (Kueppers et al. 2005, Loarie et al. 2008, Wiens et al. 2009). In the case of *P. coulteri*, the SDM suggests that CWD, AET, summer maximum temperature, annual precipitation, and winter minimum temperature are all associated with the current distribution. However, we also note that the estimate of climate suitability is based on the current range, and dispersal limitation will lead to a conservative estimate of the climatic envelope as unoccupied suitable areas are not included (see discussion in Peterson et al. 2011). Furthermore, the differences in climatic suitability observed at the northern range limit and at the central high elevation populations could be due to local adaptation.

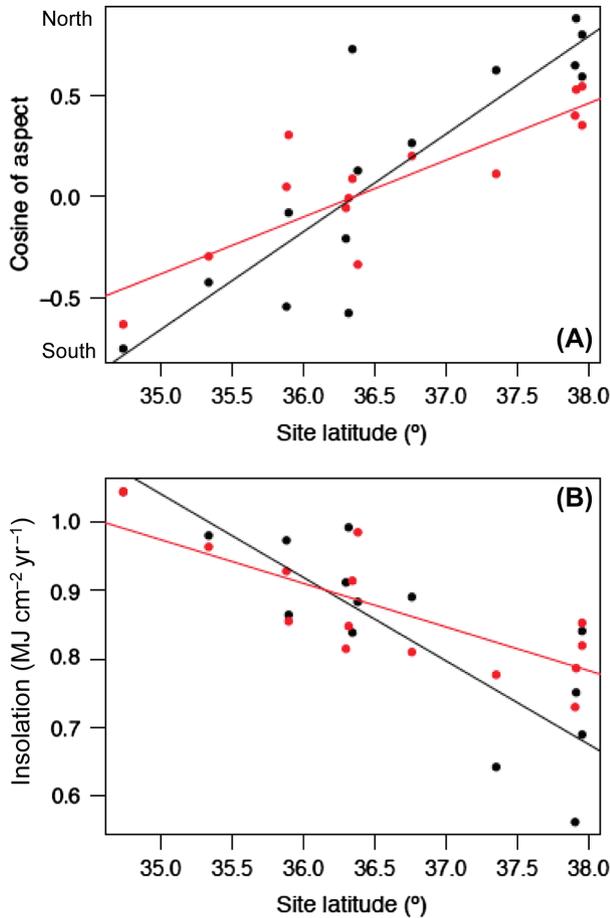


Figure 6. Site mean aspect (A) and insolation (B) at local scale *P. coulteri* habitat. Site mean latitude plotted against cosine of aspect (measured as degrees from North) and insolation shows that northern *P. coulteri* grow on more north-facing slopes that receive less yearly insolation than surrounding, unoccupied areas. Occupied points in black and unoccupied points in red. Linear regression lines of best fit follow the same color coding, with regressions done on individual points ($n = 560$), not site means. We generated site means ($n = 14$) for the average of values (aspect, insolation, and latitude) for occupied points ($n = 20$ per site), as well as for the average of values for unoccupied points ($n = 20$ per site). Analyses of covariance (ANCOVA) on linear regressions of the effect of latitude and species occupancy on aspect and insolation yield p values < 0.0001 for the latitude-species occupancy interaction.

The fate of organisms in response to climate change is determined by the particulars of the realized climate space (sensu Jackson and Overpeck 2000) – the subset of possible climates that are currently in existence. With climate change, every point in the current realized climate, with respect to summer and winter temperatures (Fig. 3D) will shift up and to the right. Overall hotter winter minimum and summer maximum temperatures will decrease the amount of preferred habitat for *P. coulteri* at the northern end of its range as there are no high elevation areas with cooler temperatures to escape to. The particular geography of California, specifically the low elevations of the Coast Ranges between Monterey County and Mendocino County, means there is very little suitable high elevation area in the north as sites for future range expansion for *P. coulteri*. For 6 of 10 future scenarios examined here, suitability declines at the northernmost limit, rather than increasing (Table 1).

Under a drier and hotter scenario (MIROC rcp-8.5), suitability for this species declines over its range and shifts closer to the coast, where maritime climate would offset regional warming, and up to higher elevations of the southern Sierra Nevada (currently unoccupied). These results are consistent with a recent bioclimatic velocity study by Serra-Diaz et al. (2013), as they also demonstrate that this species will experience a loss of climatic suitability over time and its range is expected to shrink. However, suitability for the closely related California endemic *Pinus sabiniana* increases in northern California in the Sierra Nevada Mountains (Serra-Diaz et al. 2013). Although these two species co-occur from the San Francisco Bay Area south along the Coast Ranges, *P. sabiniana*'s range stretches much further north and along the Sierra Nevada foothills (Critchfield and Little 1966). These patterns suggest that *P. sabiniana* can tolerate a much wider climatic range than *P. coulteri*.

Site level analyses

We expected to see a correlation between aspect and species occupancy (Warren 2008), and see a significant shift in the aspect of occupied sites with latitude among northern population of *P. coulteri* (Table 3). However, we expected pines at northern sites to grow on slopes that receive the highest amount of insolation (south facing and flatter slopes with more sunlight exposure) to compensate for the presumably lower regional temperatures and thus lower evaporative demand (Stephenson 1998). Surprisingly, we observed the contrary; northern, low elevation *P. coulteri* populations occupy more north-facing, low insolation slopes (Fig. 5A). This shift towards north-facing slopes is even more dramatic than would be expected simply based on the available topography, as we found an increasing difference in the aspect and insolation of occupied vs adjacent unoccupied points in these northern population. We would expect that pines growing on lower insolation sites are compensating for hotter regional climate and higher evaporative demand, but found that the northern stands experience average temperatures for the species. As our climatic analyses show that northern populations are not at the cold climatic edge of the species, this result is consistent with the lower evaporative demand (Stephenson 1998). Additionally, we expected to find that areas with high maximum regional temperatures have lower insolation values to compensate for the heat and higher evaporative demand, but the two were not correlated (Fig. 5B). We found that the northern portion of the species range, where *P. coulteri* inhabits north-facing slopes, experiences lower precipitation than other parts of the range. This could explain the unexpected low insolation values at northern occupied sites, as the species may shift to cooler slopes to offset low precipitation. Insolation will impact both daytime temperatures and water balance, but we do not have detailed data available (including soils data) to evaluate the water balance of the sites occupied by *P. coulteri*.

Occupied—unoccupied points

Pinus coulteri growing at the northern end of the range inhabit areas that are more north-facing and receive less yearly insolation than adjacent unoccupied areas (Fig. 6A, B). Occupied

areas in central portions of the range are more south facing than adjacent unoccupied areas. In other words, this species only grows in the cool microsites at the northern portion of the range, consistent with the overall shift from south-facing to north-facing slopes as one moves from the high elevation central populations to the lower elevation northern ones (Fig. 3A). Stephenson (1998) argues that in order to explain such a shift, consideration of AET and deficit is important, as coarse topographical variables do not fully capture water balance. The effect of latitude on aspect is stronger on occupied points than on unoccupied points, as evidenced by a steeper regression line slope and a significant interaction effect (Fig. 6A, Table 3). We see the same pattern with insolation (Fig. 6B), which we calculated from aspect values (see Methods). We recognize that this interaction effect could be partially explained by the fact that northern stands are located at northern aspects and so adjacent unoccupied areas by default will be less north facing. Likewise, central stands are located on southern aspects and so adjacent unoccupied areas could therefore be less south facing. However, we see that central populations receive higher annual precipitation than northern ones (Table 2), and this may explain the shift to south-facing slopes. A number of other factors could influence these local distributions patterns, and are beyond the scope of this paper. Local adaptation could result in shifts in abiotic tolerances across the species' range. Performing transplant studies would enable us to test this alternative hypothesis, as well as further examining our dispersal-limit conclusion (Ehrlén and Eriksson 2000). Shifting biotic interactions, differences in edaphic factors, and details of local water balance could all influence fine-scale distributions. Perhaps most importantly, fire is necessary for regeneration, and so plays an important role in the distribution of this species. Fire history analyses would enable us to make more definitive statements regarding climatic and topographic influences on this major disturbance, and hence on *P. coulteri* distributions.

Conclusion

Contrary to our hypotheses, we found that northern populations of *P. coulteri* are not at the cold limit of the species' climate space and dispersal appears to be limited by either the San Francisco Bay and Delta (dispersal barrier) or a migration lag since the LGM. Instead of expanding, northern populations are expected to decline with changing climate, which we hypothesize is related to a lack of contiguous higher elevation habitats. We stress the importance of considering multivariate 'realized' climate (Jackson and Overpeck 2000) and geography in moving from simple forecasts of poleward movement of taxa to a more nuanced understanding of the capacity and nature of climate change induced migration. This work suggests that in much of the world that is topographically complex, the simple assumption that northern populations represent the leading edge of species distributions should be evaluated critically and populations with the potential to migrate to higher elevations may play the most important role in species survival in a warming climate.

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Supplementary material (Appendix ECOG-00780 at <www.ecography.org/readers/appendix>). Appendix 1.