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RESEARCH ARTICLE

Rarity, geography, and plant exposure to global change in the California Floristic Province

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Abstract

Aim: Rarity and geographic aspects of species distributions mediate their vulnerability to global change. We explore the relationships between species rarity and geography and their exposure to climate and land use change in a biodiversity hotspot.

Location: California, USA.

Taxa: One hundred and six terrestrial plants.

Methods: We estimated four rarity traits: range size, niche breadth, number of habitat patches, and patch isolation; and three geographic traits: mean elevation, topographic heterogeneity, and distance to coast. We used species distribution models to measure species exposure—predicted change in continuous habitat suitability within currently occupied habitat—under climate and land use change scenarios. Using regression models, decision-tree models and variance partitioning, we assessed the relationships between species rarity, geography, and exposure to climate and land use change.

Results: Rarity, geography and greenhouse gas emissions scenario explained >35% of variance in climate change exposure and >61% for land use change exposure. While rarity traits (range size and number of habitat patches) were most important for explaining species exposure to climate change, geographic traits (elevation and topographic heterogeneity) were more strongly associated with species' exposure to land use change.

Main conclusions: Species with restricted range sizes and low topographic heterogeneity across their distributions were predicted to be the most exposed to climate change, while species at low elevations were the most exposed to habitat loss via land use change. However, even some broadly distributed species were projected to lose >70% of their currently suitable habitat due to climate and land use change if they are in geographically vulnerable areas, emphasizing the need to consider both species rarity traits and geography in vulnerability assessments.

1 | INTRODUCTION

Human activity is driving rapid biodiversity loss, with current extinction rates at least 100 times greater than background rates for some taxa (Ceballos et al., 2015). While land use change is the primary human activity driving species loss (Newbold et al., 2015), anthropogenic climate change impacts on species geographic distributions have been observed globally (Chen et al., 2011). Predictive frameworks for identifying vulnerable species are urgently needed in the face of rapid climate and land use change to anticipate where, and for which taxa, the most pressing needs for management and mitigation arise.

Spatially rare species generally face a greater risk of extinction across taxa and geographic locations than their more common counterparts (Leão et al., 2014; Ohlemüller et al., 2008; Staude et al., 2020). The ecological and evolutionary mechanisms that produce spatial rarity vary, and to capture these nuances, Rabinowitz (1981) proposed a rarity framework based on three species characteristics: geographic range size, degree of habitat specificity (i.e., niche breadth), and local abundance. Although interrelated, each of these characteristics describes distinct features of a species' spatial rarity and may uniquely influence a species' vulnerability to environmental change. Range size has frequently been identified as one of the most important predictors of extinction risk (Leão et al., 2014; Payne & Finnegan, 2007), with geographically restricted species often being associated with the highest extinction risks. In terms of spatial rarity and extinction vulnerability, small-ranged species with narrow niche breadths overwhelmingly face the highest vulnerability to environmental change (Johnson, 1998; Payne & Finnegan, 2007; Thuiller et al., 2005).

Species persistence under global change also depends on the spatial configuration of habitat, including patch size and degree of isolation from other patches. Habitat patchiness, measured by the number of patches or the distance between patches, can protect or insulate species from the negative impacts of environmental change due to "risk-spreading", that is, the risk of habitat loss is spread, and therefore diluted, across the landscape (Blowes & Connolly, 2012). This is especially true when the effect of a system perturbation is spatially "patchy", as is often the case with land use change and can be true for climate change in areas with complex terrain that modifies climate. However, habitat patchiness may reflect ongoing habitat loss due to changing climates (Petit et al., 2003) and the conversion of natural land to urban or agriculture use, historical legacies that may make species more susceptible to continued habitat loss under future global change. Although not included in traditional rarity frameworks, aspects of fragmentation help describe the spatial rarity of suitable habitat across species ranges and are considered rarity traits in this context.

Climate and land use change impacts are spatially structured, meaning that some species will be more vulnerable to their effects than others based on their geographic context. Distance to the coast, topography, and elevation are components of a species' physical environment that influence the magnitude of environmental change they will experience. However, the effect of a geographic factor on species vulnerability can vary. For example, while proximity to coastlines may offer the benefits of relatively stable or even cooling climates (Lebassi et al., 2009), terrestrial species with suitable habitat projected to shift closer to the coast under climate change may be more vulnerable to range reductions than species projected to move inland (Broennimann et al., 2006). Additionally, urban development is concentrated and projected to increase along coastlines in our focal study area—California, USA—making coastal species especially vulnerable to habitat loss via land use change.

Topographically complex landscapes can provide climatically stable refugia, for example, north-facing slopes and cold air drainages, which may offer species refuge under rising temperatures (Serra-Diaz et al., 2015), as they have during past climate change (Dobrowski, 2011), while also reducing climate velocities (Loarie et al., 2009). Furthermore, topographically complex areas are generally less likely to face urban and agricultural development than flatter areas (Syphard et al., 2005), potentially reducing species vulnerability to land use change in these areas. Additionally, elevational position influences species vulnerability to environmental change. Interactions between declining water availability and rising temperatures in mountainous areas may exacerbate drought conditions and reduce suitable habitat for high-elevation species in water-limited Mediterranean-type climates, such as those found in the Sierra Nevada, California (McCullough et al., 2016; Figure 1).

Exposure is a key component of species vulnerability to global change that quantifies the magnitude of suitability change expected to be experienced by a species (Dawson et al., 2011) and is often inferred from changes in a species' environmentally suitable space (Garcia, Araújo, et al., 2014). Disentangling the relative importance of rarity and spatial context for determining species exposure to global change is important for improving conservation decision-making, particularly if the relative contributions of these traits vary depending on the environmental change driver. In our research, we asked the following questions for a set of 106 plant species in the California Floristic Province (CFP): (a) how do range-wide rarity and geographic traits relate to plant species exposure to future climate and land use change? and (b) how do species rarity and geographic traits interact to influence climate and land use change exposure? In this study, we measured climate and land use change exposure as the total proportional loss of suitable habitat across the study species' currently occupied ranges (Garcia, Cabeza, et al., 2014) because this metric does not rely on assumptions about dispersal capacity to reach new suitable areas outside the current range.

2 | METHODS

2.1 | Study area and species

With > 2000 endemic vascular plant species (Baldwin et al., 2012), the CFP, defined as the area of western North America with a Mediterranean-type ecosystem located almost entirely within

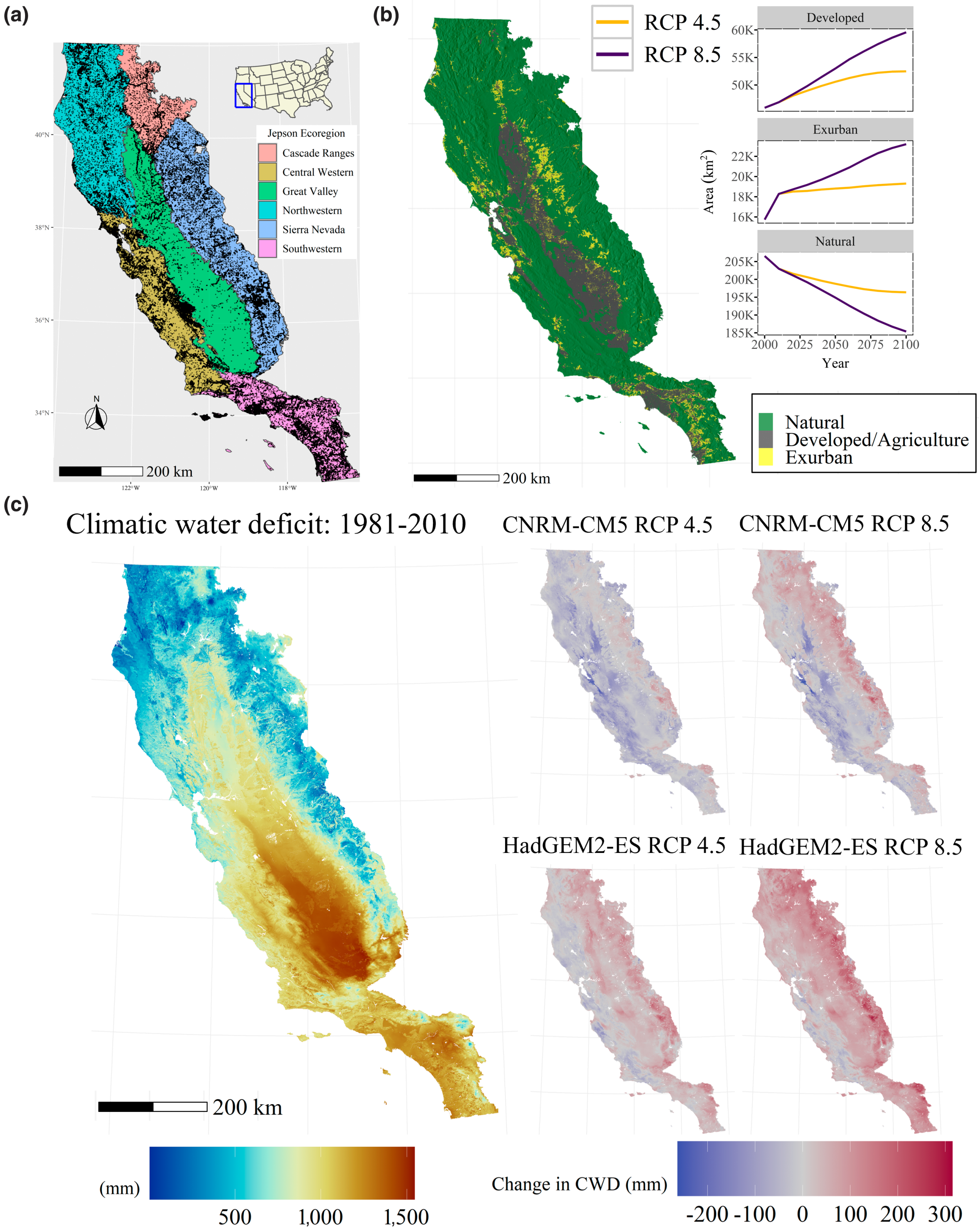

FIGURE 1 California Floristic Province (CFP) within California. (a) Jepson Ecoregions and 76,266 survey locations for plant species presence–absence data. (b) Map of land use patterns in the CFP in the year 2000 and area trends for each land use class (natural, developed and exurban) between 2000–2100 under two emissions scenarios: representative concentration pathway (RCP) 4.5 and RCP 8.5. (c) Climatic water deficit (CWD; the difference between potential and actual evapotranspiration)—an important driver of vegetation distributions in water-limited, Mediterranean-type ecosystems—in the CFP for the historical period 1980–2010 and projected change for the period 2070–2099 under two climate models (CNRM-CM5 and HadGEM2-ES) and two emissions scenarios (RCP 4.5 and 8.5).

California, is a topographically diverse biodiversity hotspot (Myers et al., 2000). Stretching across 10 degrees of latitude and 4000 metres of elevation, the California portion of the CFP (Figure 1) supports a wide variety of terrestrial vegetation systems. This region faces unique pressure from both climate and land use change, with temperatures projected to increase 2–7 °C and developed land area projected to more than double between the late 20th–early 21st centuries and the year 2100 (Pierce et al., 2018; Sleeter et al., 2017). Our assessment was based on 106 plant species that are endemic to the CFP and that represent different life-forms, range sizes (<200 to >30,000 km^2) and range locations (Serra-Diaz et al., 2014). While not a random sample, these species include about 5% of the endemic flora and were selected to encompass the broad range of life histories and geographies found in the CFP (Supporting Information Appendix S1, Table S1.1).

2.2 | Species and environmental data

For 84 of 106 species, we compiled species presence–absence records from vegetation surveys (Hannah et al., 2008) and Calflora.org between 1980–2020. For the 22 species with too few presence–absence records from the vegetation surveys, we created a presence-only database using the Consortium of California Herbaria, the Global Biodiversity Information Facility (DOI: 10.15468/dl.nrdmke), the Integrated Digitized Biocollections, and the Botanical Information and Ecology Network. The number of presences available for modelling after filtering ranged from 12 to 4646 across the 106 species (see Supporting Information Appendix S2, Table S2.4 for data cleaning procedure; Table S2.1 for data sources). All occurrence data were restricted to the study extent (i.e., CFP).

We calibrated species distribution models (SDMs) using climatic, hydrological, terrain and soil predictors associated with plant distributions, especially in water limited ecosystems like California (Stephenson, 1998). Climatic and hydrological predictors included climatic water deficit, actual evapotranspiration, minimum monthly temperature, and wet- and dry-season precipitation averaged from annual values for the years 1981–2010 at a 270-m spatial resolution. These variables are derived from the California Basin Characterization Model (BCM), which uses fine-scale temperature interpolations and soil characteristics to capture the hydroclimatic effects of topography (Flint et al., 2013; Hannah et al., 2014) and has been used in recent research to project the future distributions of plant species in California under climate change (Thorne et al., 2017) (Supporting Information Tables S2.2 and S2.3).

Including edaphic variables as predictors in SDMs produces more comprehensive models based on factors limiting terrestrial plant distributions, especially when projecting models under climate change (Kueppers et al., 2005; Velazco et al., 2017). We obtained 10-m resolution soil pH, available water holding capacity, soil depth and percent clay from the gridded National Soil Survey Geographic Database (gNATSGO, Soil Survey Staff, 2020). For species with >50 records, we included landform types (15) based on hillslope position and dominant soil formation processes (Theobald et al., 2015), while topographic heterogeneity [continuous variation in elevation, obtained from a 90-m digital elevation model (DEM)] was used instead for species with <50 records. We resampled the soil and terrain variables to match the spatial resolution of the climate data (270 m), using nearest neighbour resampling for the categorical landform data and a bilinear approach for the continuous variables (Supporting Information Table S2.2). We also assumed that soil and landform conditions will remain constant through time and used them to project models in space for both the current and future climatic conditions.

To assess climate change exposure for the period 2070–2099, we selected two global circulation models (GCMs), CNRM-CM5 (Centre National de Recherches Meteorologiques climate model version 5) and HadGEM2-ES (Hadley Centre Global Environmental Model version 2- Earth system configuration), and two emissions representative concentration pathways (RCPs), RCP 4.5 and 8.5 (IPCC, 2013). The GCMs are among the 10 recommended by California's Fourth Climate Change Assessment and encompass the variability in climate change projections for California (Pierce et al., 2018), ranging from warm and wet (CNRM-CM5) to hot and dry (HadGEM2-ES), with a reduction in greenhouse gas emissions under the RCP 4.5 scenarios, and increasing greenhouse gas emissions ("business as usual") under the RCP 8.5 scenarios. All future climate data were produced by the BCM at a 270-m spatial resolution.

2.3 | Land use data

To assess the impact of current and future land use, we used projections for the HadGEM2-ES RCP 4.5 and 8.5 scenarios from the Integrated Climate Land Use Scenario (ICLUS), which are based on a human demographic growth model and are consistent with the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emission Scenarios (Bierwagen et al., 2010; Theobald, 2005). These land use change scenarios predict increases in urban and exurban development and decreases in agricultural and forest lands (Figure 1). To simplify each land use category's impact on habitat suitability produced by the SDMs, we estimated that cells with natural land uses would have no impact on habitat suitability, cells within the exurban category would experience a 50% reduction in habitat suitability (e.g., an exurban grid cell with an initial suitability value of .75 is assigned a new value of .375) and cells classified as developed would become unsuitable (suitability value of zero) (Supporting Information Table S2.5).

2.4 | Species distribution models

We selected eight SDM algorithms for ensemble predictions: generalized linear models, generalized additive models, boosted regression trees, random forests, artificial neural networks, support vector machines, maximum entropy, and gaussian process

(Franklin, 2010). The last two algorithms were only used for presence-only models. Ensembles, in which predictions of individual algorithms are combined to produce a consensus distribution, can reduce model uncertainty and improve model transferability (Araújo & New, 2007). For each model, we applied the model-specific suitability value that maximized the sum of sensitivity and specificity as a threshold, retaining continuous suitability values above the threshold and assigning 0 suitability values to those cells below the threshold. This method removes areas with low habitat suitability while retaining variation in suitability within remaining species' habitat (Muscatello et al., 2021), and allowed us to later define discrete species' ranges to calculate the number of patches and patch isolation. The resulting continuous suitability values were averaged across all models to produce a "mean above threshold" ensemble. We produced 786 models (84 of presence–absence species ×7 algorithms/ensemble + 22 of presence-only species ×9 algorithms/ensemble) with 3144 projections (2 GCMs ×2 RCPs).

Our exposure analysis focused on the temporal dynamics of suitability within each species' currently occupied ranges. When a model is projected outside the calibration area, patches with high suitability may be predicted far from a species' current =distribution, leading to "overprediction" (Mendes et al., 2020; Velazco et al., 2020). Therefore, we constrained current and future model predictions by selecting only suitability patches (contiguous suitable pixels) that contained at least one occurrence (Mendes et al., 2020). All SDMs were calibrated and evaluated using the *flexsdm* package in R (R Core Team 2021; Velazco et al., 2022; see Supporting Information Appendix S2 and Table S2.4 for details on modelling).

2.5 | Rarity and geographic traits

We calculated four species-level rarity traits based on species occurrence data and currently occupied suitable habitat maps produced by the ensemble SDM procedure outlined previously. Rarity traits included range size, niche breadth, number of patches and patch isolation. Range size was calculated as the area in km^2 encompassed by the minimum convex polygon that contained all species' occurrences used for modelling. We calculated niche breadth with the hydroclimatic and soil variables used to build SDMs, adapting methods developed by Vela Díaz et al. (2020) (Supporting Information Appendix S3). We standardized all environmental variables across the extent of the CFP to z-scores (mean = 0, SD = 1) to account for differences in units of measurement and variance in the environmental variables. To reduce collinearity in the environmental data, we performed separate principal components analyses (PCAs) for (a) climate and (b) soil variables and selected the principal components that explained 95% of the variation in each (Supporting Information Figure S3.1). For each species, we calculated the sum of the squared difference between the environmental value of each occurrence record and the environmental mean value of all occurrence records for that species. The niche breadth of a species represents the sum of this value across all environmental variables divided by the number of occurrence records for that species. To calculate the number of habitat patches and average patch isolation for each species' range, we first binarized currently occupied suitable habitat maps using the threshold that maximized the sum of model sensitivity and specificity. We then used functions from the *landscapemetrics* R package to calculate the number of habitat patches and the coefficient of variation of the Euclidean nearest-neighbour distance between each patch (patch isolation) for each binarized habitat map (Hesselbarth et al., 2019). Geographic traits included distance to coast, elevation, and topographic heterogeneity. We used a 90-m DEM to calculate topographic heterogeneity as the range in elevation values from a centre cell and the three-cell neighbourhood immediately surrounding it. These values were then converted to a 0–1 scale using the standard deviation of the range of values across the study area. To summarize species-level geographic traits, we averaged the values for each of these variables across all occurrences for each species (see Supporting Information Table S2.2 for data sources). More information about the rarity and geographic traits and our predictions for the relationships between these traits and exposure are summarized in Table 1.

2.6 | Calculating exposure to climate and land use change

We defined exposure in a 270-m grid cell within a species' currently occupied range as habitat suitability change between the baseline (1980–2010) and future time period (2070–2099) based on SDM predictions and land use patterns:

$$\text{Exposure}_c = \text{baseline habitat suitability}_c - \text{future habitat suitability}_c \quad (1)$$

In this framework, exposure varies continuously and is not dependent on binary thresholds, that is, unsuitable versus suitable (Guillera-Arroita et al., 2015). To summarize species-level range exposure, we calculated habitat suitability as the sum of grid cells (c) across the total number of grid cells (n) in the spatial projections of the species' occupied area (Leão et al., 2021):

$$\text{Habitat suitability}_{\text{sum}} = \sum_{c=1}^{n} \text{environmental suitability within occupied range}_c \quad (2)$$

Range exposure represents the sum of change in suitability values from the baseline and future time periods proportional to the baseline suitability averaged across the two GCMs for each RCP:

$$\text{Range exposure} = \left(\frac{\text{baseline habitat suitability}_{\text{sum}} - \text{future habitat suitability}_{\text{sum}}}{\text{baseline habitat suitability}_{\text{sum}}} \right) \quad (3)$$

We evaluated species exposure to climate change only (CC), land use change only (LUC), and climate and land use change combined (CC+LUC) (Figure 2). Using this framework, range exposure values >0 correspond to a decrease in habitat suitability, while range exposure values <0 indicate an increase. A species projected to experience a

TABLE 1 Species traits that are related to climate and land use change exposure (based on Franklin et al., 2021; Pearson et al., 2014) and predictions about how each trait is related to plant vulnerability to climate and land use change in the California Floristic Province (CFP)

	Attribute	Metrics	Predictions
Rarity traits	Range size	Area of minimum convex polygon around occurrences (km^2)	Smaller range size—greater exposure to climate and land use change
	Niche breadth	Abiotic environmental tolerances based on climate, terrain and soil values (270-m resolution) at species occurrences (Vela Díaz et al., 2020)	Narrow niche breadth—greater exposure to climate change
	Range fragmentation	Number of suitable habitat patches, average patch isolation—based on ensemble SDM of currently occupied habitat (Hesselbarth et al., 2019)	Higher range fragmentation—less exposure to land use change (risk spreading) and greater climate change exposure
Geographic traits	Distance to coast	Average distance (km) between species occurrences and the coastline (NASA Earth Data)	Closer to the coast—less climate change exposure and greater land use change exposure
	Range topography	Average topographic heterogeneity[a] of species occurrences (0–1; 90 m)	Higher topographic complexity—less exposure to climate and land use change
	Elevation	Average elevation (m) of species occurrences (90 m)	Higher elevation—greater exposure to climate change and less exposure to land use change

Note: SDM = species distribution model.

[a] Range in elevation values from a centre cell and the three-cell radius immediately surrounding it, rescaled to 0–1 using the standard deviation of the range of values across the study area.

complete loss of suitable habitat within its current range would have a range exposure value of 1.

2.7 | Statistical analyses

Exploratory analyses revealed that our data demonstrated non-homogeneity of variance and skewed distributions (Supporting Information Figure S4.2), so we selected generalized additive models for location, scale and shape (GAMLSS) as the regression framework to test our predictions about the relationships between individual species' spatial range traits and their exposure to climate and land use change (Table 1). GAMLSS is a flexible statistical modelling approach with a variety of distribution families and distribution parameters (location, scale, shape; Rigby & Stasinopoulos, 2005; Supporting Information Appendix S4 for modelling procedure).

Because of multicollinearity between two geographic traits, mean elevation and distance to coast, we first estimated the GAMLSS between exposure and each trait individually, including RCP scenario as an interaction term in each model to evaluate different relationships between spatial range traits and exposure under the two emissions scenarios, and species as a random intercept. While the GAMLSS approach allows us to assess the relationship between each species' trait and exposure, we also wanted to quantify the unique and shared variance in exposure explained by rarity traits, geographic traits, and RCP. To do this, we performed variance partitioning via partial regression using the *vegan* R package (Oksanen et al., 2021). Species are phylogenetically related, violating the assumption of data independence, and this can lead to overestimating degrees of freedom in approaches like GAMLSS. We examined Moran's *I* phylogenetic correlograms for the residuals of each GAMLSS using a phylogenetic tree created for California plant species (Thornhill et al., 2017; Supporting Information Appendix S5).

To explore interactions between species' traits and exposure, we also implemented a decision tree approach, which has been used to interpret extinction risk factors (Leão et al., 2014). Decision trees iteratively partition data into subgroups based on values of predictor variables, with each resulting group being more homogenous in terms of the response variable, as measured by the Gini index (Breiman et al., 1984). They can also handle multiple correlated predictor variables and rely on fewer assumptions than more traditional regression approaches, that is, distribution of the response and predictor variables and data independence. Because the goal of our decision tree analysis is to understand how the interactions between multiple spatial range traits influence exposure, and not to make predictions, we did not apply any complexity costs to the final decision tree and present the "full grown trees" in our results. We evaluated how complexity influenced the error rate using 10-fold cross-validation (Supporting Information Figure S6.4).

3 | RESULTS

We modelled the spatial distributions and exposure of 106 species, including 48 shrubs, 32 trees and 26 herbs. SDMs performed well across species and algorithm types [area under the curve (AUC): mean = .88 ± .06 *SD*; true skill statistic (TSS): mean = .68 ± .14 *SD*; Boyce index: mean = .87 ± .12 *SD*; Sorensen: mean = .58 ± .25 *SD*;

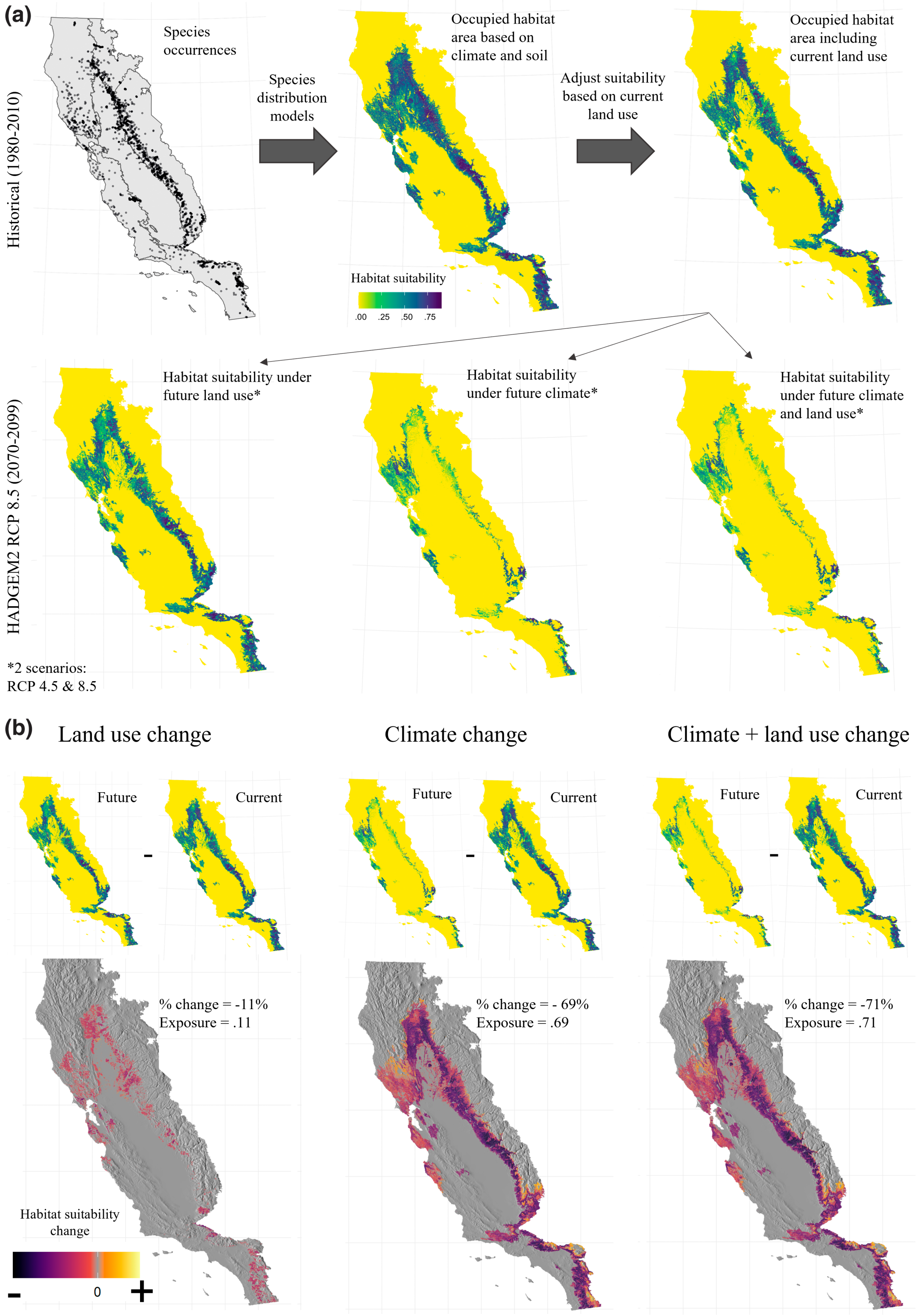

FIGURE 2 Workflow for modelling species' occupied suitable habitat under the baseline (1980–2010) conditions and estimated exposure for the future time period (2070–2099) under climate and land use change scenarios (a); and estimating species exposure to land use change, climate change [for each representative concentration pathway (RCP)], and climate plus land use change, shown overlaid on a digital elevation model (DEM)-derived hill shade for the study area (b). For our analysis, we averaged the exposure values from the two climate change global circulation models (GCMs; HadGEM2-ES and CNRM-CM5).

F-measure on presence-background data (FPB): mean = .92 ± .50 *SD*] (Supporting Information Figure S2.1).

3.1 | Exposure to climate and land use change

Across all species and the two emissions scenarios, mean exposure was lowest for land use change alone (.10), followed by climate change alone (.27) and highest for the combined effect of both (.34). As expected, species exposure was greater for the RCP 8.5 than the RCP 4.5 for climate change (mean .33 vs. .21), land use change (.12 vs. .07) and the combined effect of both (.41 vs. .26) (Figure 3).

3.2 | GAMLSS results

The univariate GAMLSS showed strong evidence that patch isolation, elevation, and distance to coast are each positively associated with exposure to climate change, while number of patches, and rarity trait niche breadth, are negatively associated with climate change exposure (Table 2). Range size showed evidence of quadratic relationships with exposure to climate change, where small-ranged and large-ranged species were the most exposed to climate change (Figure 4). There was no evidence of a relationship between mean topographic heterogeneity and climate change exposure in the overall model. However, we found a significant interaction between topographic heterogeneity and RCP emissions scenario, where topographic heterogeneity had no relationship with climate change exposure under RCP 4.5 but was negatively associated with exposure under RCP 8.5 (Figure 4). There was also evidence of an interaction between range size, number of habitat patches, topographic heterogeneity, and distance to coast and emissions scenario. R^2 values indicate that range size, along with RCP, explained the most variation in climate change exposure, followed by number of patches (Table 2).

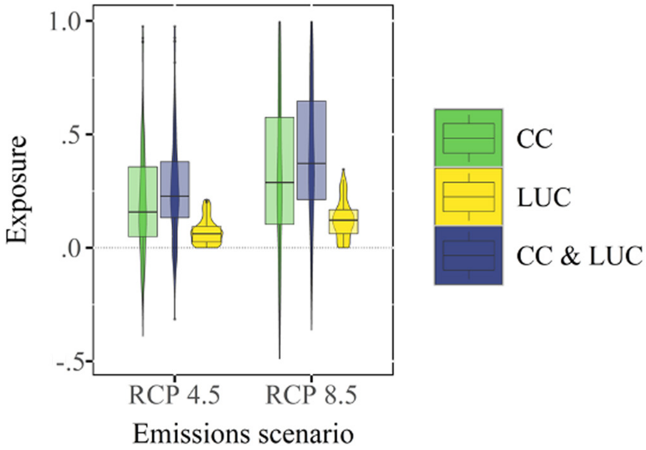

FIGURE 3 Boxplots summarizing species-level exposure under climate change (CC), land use change (LUC) and the combined effect of climate and land use change (CC & LUC) for each emissions scenario. Positive exposure values indicate a decrease of suitability. The boxplots show the median value along with the first (lower) and third (upper) quartiles (the 25th and 75th percentiles, respectively).

We found strong evidence that niche breadth, patch isolation, elevation, and average topographic heterogeneity were negatively associated with land use change exposure. There was moderate evidence that average distance to coast is negatively associated with land use change exposure, as well (Table 2). Conversely, the number of habitat patches was positively associated with land use change exposure. In contrast to the results for climate change exposure, species with intermediate range sizes were the most exposed to land use change (Figure 3). Half of the model terms showed evidence of an interaction with RCP (Table 2). Generalized R^2 values showed that elevation explained the most variation in land use change exposure followed by number of patches and distance to coast (Table 2). The relationships between species' rarity and geographic traits and exposure to combined climate and land use change were similar to the patterns under climate change alone (Supporting Information Table S4.1, Figure S4.3). GAMLSS model residuals showed no evidence of phylogenetic autocorrelation (Supporting Information Figure S5.2), suggesting that our results were not affected by phylogenetic relatedness between species.

3.3 | Variance partitioning

Overall, rarity traits, geographic traits and RCP emissions scenario explained 35.2 and 61.9% of the variance in climate change and land use change exposure, respectively (Figure 5). While rarity traits explained the most variance in climate change exposure (14.1%), geographic traits were most important for explaining species' exposure to land use change (41.1%).

3.4 | Decision tree analysis

Decision tree analysis revealed that range size was the most important predictor of climate change exposure under the RCP 8.5 emissions scenario, as indicated by the first tree split, with small-ranged species (<14,000 km^2) being more exposed than species with larger ranges (Figure 6). Subsequent splits indicated that species with higher mean topographic heterogeneity were less exposed to climate change than species in topographically homogenous areas. We observed a similar pattern for the number of patches, where species with more habitat patches were less exposed than species with fewer habitat patches across their ranges. Other splits indicated that species that were closer to the coast, had broader niches or were at lower elevations tended to be less exposed than species far from the coast, at higher elevations or that occupied narrow environmental niches. The least climate exposed groups of species (far left nodes, exposure = −.051 to .012), were those with large range sizes, many habitat patches and wide niche breadths, and that were located less than 46 km from the coast with high mean topographic heterogeneity across their ranges (*n* = 26). However, the most exposed group

TABLE 2 Results of generalized additive models for location, scale and shape (GAMLSS) for species rarity and geographic traits (predictors) and the response variables range-wide climate change and land use change exposure

		Climate change exposure				Land use change exposure			
		R^2	Estimate	*SE*	*p*	R^2	Estimate	*SE*	*p*
Rarity Traits	Range size	.31	−0.78***	0.009	<.001	.39	1.2	0.27	<.001
	Range size^2		0.92***	0.12	<.001		−2.53	0.21	<.001
	Niche breadth	.12	−0.02***	0.006	.001	.05	−0.19***	0.01	<.001
	Number of patches	.29	−0.09***	0.008	<.001	.57	0.36***	0.02	<.001
	Patch isolation	.12	0.208	0.02	<.001	.25	−1.85***	0.08	<.001
Geographic Traits	Elevation	.17	0.0002	0.00001	<.001	.80	−0.002	0.00005	<.001
	Topographic heterogeneity	.10	−0.01***	0.04	.75	.32	−5.55	0.12	<.001
	Distance to coast	.13	0.001	0.0001	<.0001	.58	−0.02	0.0005	<.0001

Note: R^2 indicates the proportion of variance in exposure explained by each rarity and geographic trait and RCP scenario. Exposure is based on the proportion of habitat suitability loss within species' currently occupied ranges, where 1 = 100% decrease. Estimates, standard errors and *p*-values are based on individual GAMLSS between spatial traits and species exposure. Asterisks denote the significance of the interaction between each spatial range trait and RCP: ***$p < .001$.

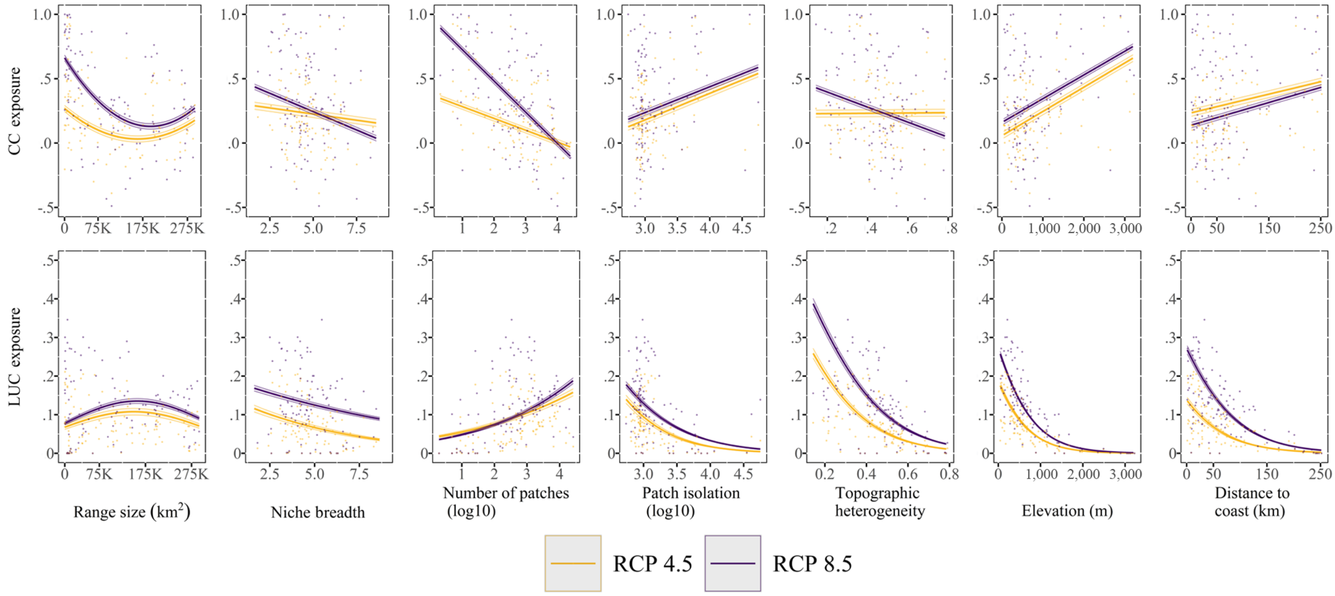

FIGURE 4 Fitted response curves for the generalized additive models for location, scale and shape (GAMLSS) relating rarity and geographic traits to climate change (CC) and land use change (LUC) exposure under emissions scenarios representative concentration pathway (RCP) 4.5 and RCP 8.5. Upper and lower pointwise standard error curves are shown in each plot (shaded areas).

of species (exposure = .78, *n* = 17) had small ranges and low mean topographic heterogeneity.

For land use change exposure under RCP 8.5, the first split is determined by the mean elevation of species' ranges, where species at higher elevations were less exposed to land use change than those at lower elevations. Species with higher mean topographic heterogeneity were less exposed than species in locations with lower average heterogeneity. Splits based on range size indicated that species with small range sizes were more exposed than widespread species. The least exposed group of species (exposure = .017–.073, *n* = 35) were located at mean elevations greater than 771 m. However, the species that were predicted to be most vulnerable to land use change (exposure = .24, *n* = 17) were located at low elevations, in topographically homogenous areas, and had range sizes smaller than 71,000 km^2.

4 | DISCUSSION

In this study, we (a) measured exposure (change in habitat suitability within species' current geographic ranges) to climate and land use change for 106 plant species in the CFP, for two emissions scenarios for the time period 2070–2099, and (b) related rarity and geographic traits to species' range-wide exposure under future climate and land

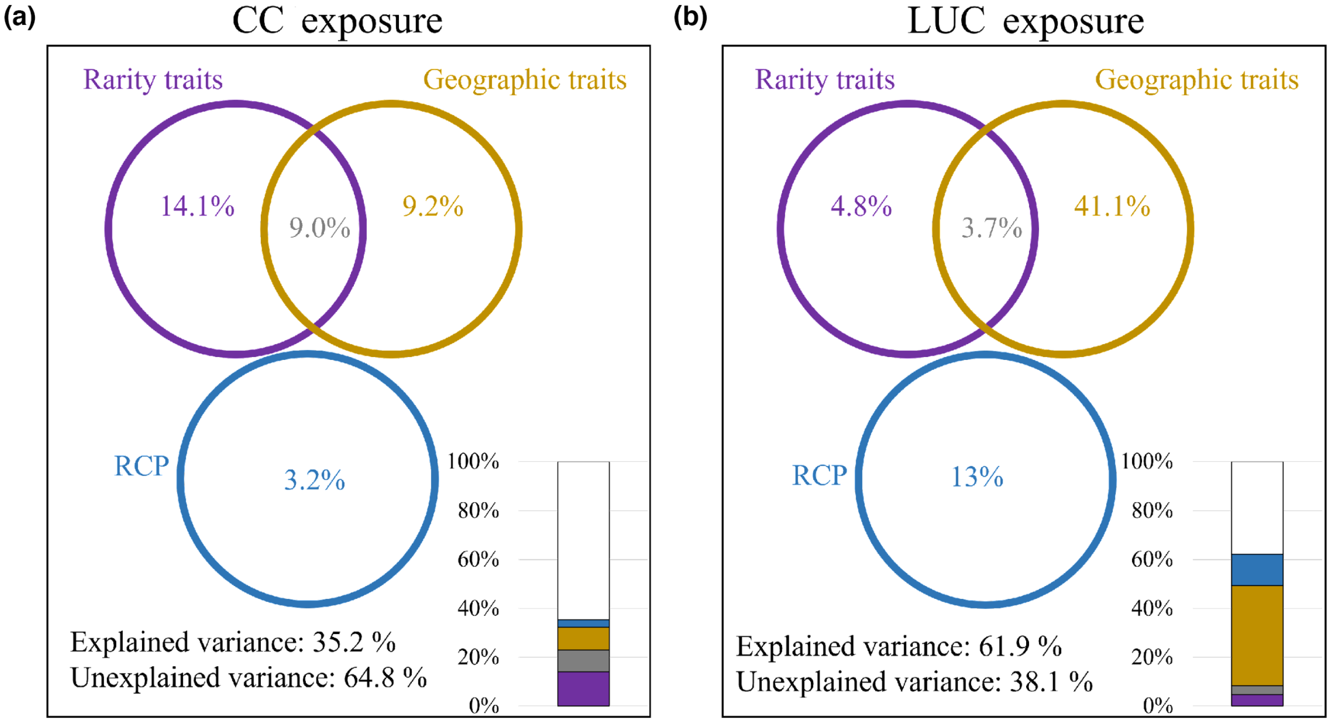

FIGURE 5 Proportion of variance in exposure to climate change (CC; a) and land use change (LUC; b) explained by rarity traits (range size, niche breadth, number of habitat patches and patch isolation), geographic traits (mean elevation, topographic heterogeneity and distance to coast), and representative concentration pathway (RCP) emissions scenario. Overlapping areas indicate shared variance between traits, while non-overlapping areas indicate no shared variance.

use change. We found that exposure to future climate and land use change varies among plant species in the CFP, with habitat suitability losses up to 100% for some species and gains up to 36% for others by the end of the 21st century. The average projected suitability loss under both climate and land use change ranged from 26% under RCP 4.5 to 41% under RCP 8.5. Rarity and geographic traits explained >35% of the variance in climate change exposure and >61% of variance in land use change exposure. Our results supported some but not all our predictions about the relationships between species traits and their exposure to climate and land use change (Table 1).

4.1 | Rarity traits and exposure

Species with small ranges were the most exposed to both climate and land use change, especially under the "business-as-usual" (RCP 8.5) higher emissions scenario (Figures 4 and 6). This finding is supported by past research that found species with small range sizes face the highest extinction risks (Chichorro et al., 2019; Pearson et al., 2014), even when other aspects of rarity, that is, habitat type and abundance, are considered (Harnik et al., 2012). Species with small geographic ranges often occupy rare and/or cooler, relict climates that may disappear rapidly under climate change (Ohlemüller et al., 2008). The heightened vulnerability of small-ranged species to both climate and land use change is particularly important in the CFP, where >60% of endemic plant species have range sizes <10,000 km^2 (Thorne et al., 2009). However, we found that the relationship between range size and exposure was not linear or even monotonic. Our results indicate that widespread species may be more exposed to climate change than species with intermediate-sized ranges, a pattern that was also found for European plant species (Thuiller et al., 2005) but remains poorly understood. A closer look at the most exposed yet widely distributed species in our study system provides some insight into this complex pattern. Widespread species in the CFP that may face high levels of habitat decline due to both climate and land use change (>70% exposure) include California buckeye (*Aesculus californica*) and blue oak (*Quercus douglasii*), two tree species whose distributions are concentrated in the foothills of the Coast Ranges and the western Sierra Nevada regions that are predicted to face rapid climate change as well as exurban development during the next century (Figure 1). Furthermore, while species with large range sizes tend to have broader environmental niches, homogenous environmental conditions may be prevalent across a region and therefore contain widespread species with narrow environmental affinities (Meyer & Pie, 2018), as we found for both blue oak and California buckeye. This finding highlights that broad spatial distributions may not buffer species from the consequences of global change, especially if their ranges are in highly vulnerable areas.

Although niche breadth and range size were positively associated for our study species (r = .44; Supporting Information Figure S4.1) and across taxa in previous research (Slatyer et al., 2013), they had

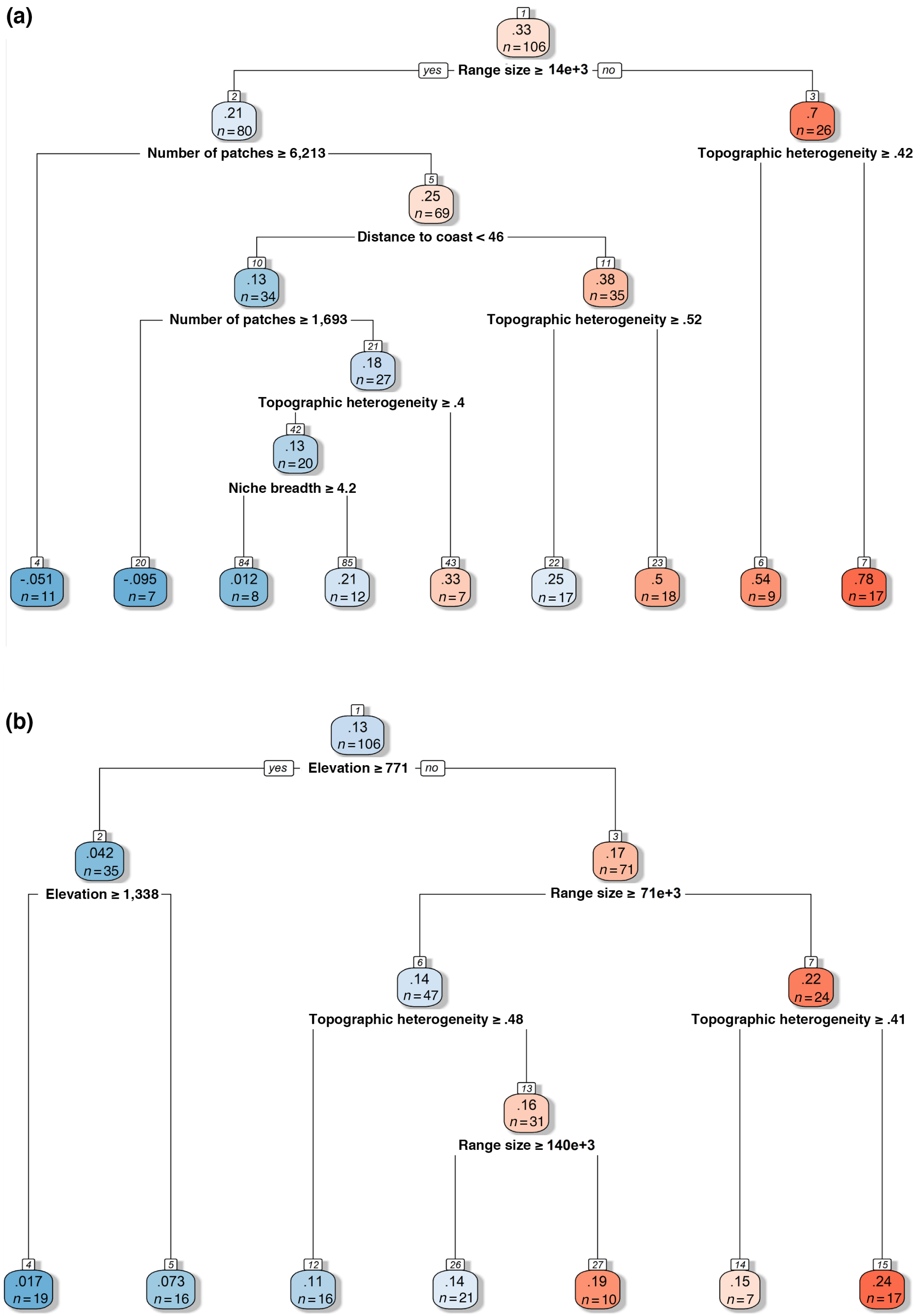

FIGURE 6 Decision tree showing exposure to (a) climate change and (b) land use change based on species rarity and geographic traits under the representative concentration pathway (RCP) 8.5 emissions scenario (see Supporting Information Figure S6.3 for RCP 4.5). In each node, the top number indicates the average exposure of the species in that group, that is, overall species had an average climate change exposure of .33 in RCP 8.5, and the second number (*n* = #) indicates the number of species in that group. The decision criteria are located below each node, where groups to the left meet that condition ("yes") and groups to the right do not ("no"). For example, all species grouped to the left of the first node in the first decision tree (a) have range sizes greater than 14,000 km^2, while those to the right have smaller range sizes. For each branch split, species to the right are more exposed than species to the left. Numbers at the top of each node correspond to the branch order, where gaps between numbers indicate branches that were pruned during model fitting.

different relationships with species exposure, emphasizing the need to consider both when conducting vulnerability analyses based on species traits. Species with broad niches tended to be the least exposed to both climate and land use change, though the relationships were highly variable (Figure 4). Anthropogenic change is already causing declines in habitat specialists globally (Clavel et al., 2011), and species with broad environmental tolerances may be more resilient to changing environmental conditions than specialist species (Broennimann et al., 2006). Interestingly, our decision tree indicated that niche breadth was only important for predicting climate change exposure in specific biogeographic contexts. For species with intermediate to large range sizes, an intermediate number of habitat patches, near the coast, and in topographically heterogeneous areas, those with narrow niches were associated with higher climate change exposure (Figure 5). However, we found that some species with narrow niches defy this pattern and are predicted to face relatively low climate change exposure, including big pod ceanothus (*Ceanothus megacarpus*), California brittlebush (*Encelia californica*), purple sage (*Salvia leucophylla*), California goldenbush (*Ericameria ericoides*), and alpine gooseberry (*Ribes lasianthum*). The first four species have relatively large range sizes concentrated along the coast of California, while alpine gooseberry's distribution is characterized by high topographic heterogeneity—all factors that may reduce species vulnerability to global change. These instances highlight species for which geography may mediate the relationship between niche breadth and species vulnerability to global change.

Regarding habitat configuration, species with fewer habitat patches and more dispersed ranges, that is, higher patch isolation, were associated with higher levels of climate change exposure. Fewer habitat patches may indicate that a species occupies only a few, restricted habitat types, magnifying its climate change risk. We found that the number of habitat patches was positively, though not perfectly, related to measures of range size ($r = .39$; Supporting Information Figure S4.1), and this metric complemented range size as a determinant of climate change exposure in our decision tree. Among our study species, those with large range sizes (≥14,000 km^2) and many habitat patches (≥6213) were associated with the lowest levels of climate change exposure (5% average gain in habitat suitability, $n = 11$). Habitat dispersion, that is, patch isolation, may reflect ongoing range disjunction due to past climate fluctuations (Petit et al., 2003) and is predicted to increase as a result of anthropogenic climate change (Jackson et al., 2015). While scattered distributions may have once reflected refugia during past climate change in California (Millar, 2012), we found that several species with isolated distributions, such as giant sequoia (*Sequoiadendron giganteum*), Parry pinyon (*Pinus quadrifolia*) and foxtail pine (*Pinus balfouriana*), were predicted to be highly exposed to climate change (>86% average habitat suitability loss under RCP 8.5). These findings suggest that climate change vulnerability assessments should consider aspects of habitat configuration alongside more commonly included traits such as range size and niche breadth.

For land use change exposure, we found that species with many habitat patches and low patch isolation were more exposed to land use change. Land use change in California is predicted to be patchy and concentrated in areas surrounding existing urban and agricultural centres as well as the foothills of the Central Valley (Sleeter et al., 2017). Patchy spatial distributions may reflect that a species' range already overlaps with developed land that will expand in the future, as was the case for the riparian California sycamore (*Platanus racemosa*), which is distributed in human-dominated areas and was projected to lose >20% habitat suitability due to land use change alone. Because land development is predicted to be concentrated in specific regions in the CFP, species with aggregated spatial distributions will be at greater risk of habitat loss if their ranges overlap with centres of development, while species with dispersed ranges may benefit from "risk-spreading" if some of their habitat is far away.

4.2 | Geographic traits and exposure

While some past research suggests that montane species are among the most vulnerable to climate change globally (Dobrowski & Parks, 2016), other work shows that lowland species will also face significant habitat loss due to rapidly warming temperatures in the next century (Hülber et al., 2020). Our findings support both paradigms in that high-elevation species were disproportionately exposed to climate change; however, many low-elevation species were also highly susceptible to the consequences of climate change (Figure 4). Complex topography is expected to provide suitable topoclimatic refugia that may facilitate species persistence under climate change (Ackerly et al., 2020), as it has during past periods of environmental change (Dobrowski, 2011). Although we found that the range-wide measure of topographic heterogeneity explains the least amount of variation in climate change exposure among the rarity and geographic traits included in this analysis (Figure 4, Table 2), it was the most frequently included trait in the decision tree analysis, despite low importance (Supporting Information Figures S6.1 and S6.2). In every instance, higher average topographic heterogeneity was associated with reduced climate change exposure (Figure 5), suggesting that while it may not represent a robust lone predictor of species vulnerability to climate change at the spatial scale of this analysis, it is important in certain contexts. Notably, low topographic heterogeneity magnifies habitat loss (54% for higher vs. 78% for lower) for species with small range sizes, highlighting how traits can interact to increase species exposure to global change.

Species' range wide elevation, topographic heterogeneity, and distance to coast explained >40% of the variance in land use change exposure among our study species, emphasizing the importance of a species' geographic context for predicting exposure to habitat conversion. We found that species located at low elevations, in areas with low topographic heterogeneity, and near the coast were the most at-risk of habitat loss due to land use change. Projected land use patterns in the CFP support these findings, in that low-elevation, flat and coastal regions will likely experience the greatest increases in urban and agricultural development by the year 2085 (Figure 7). In our study system, elevation was the most important factor in

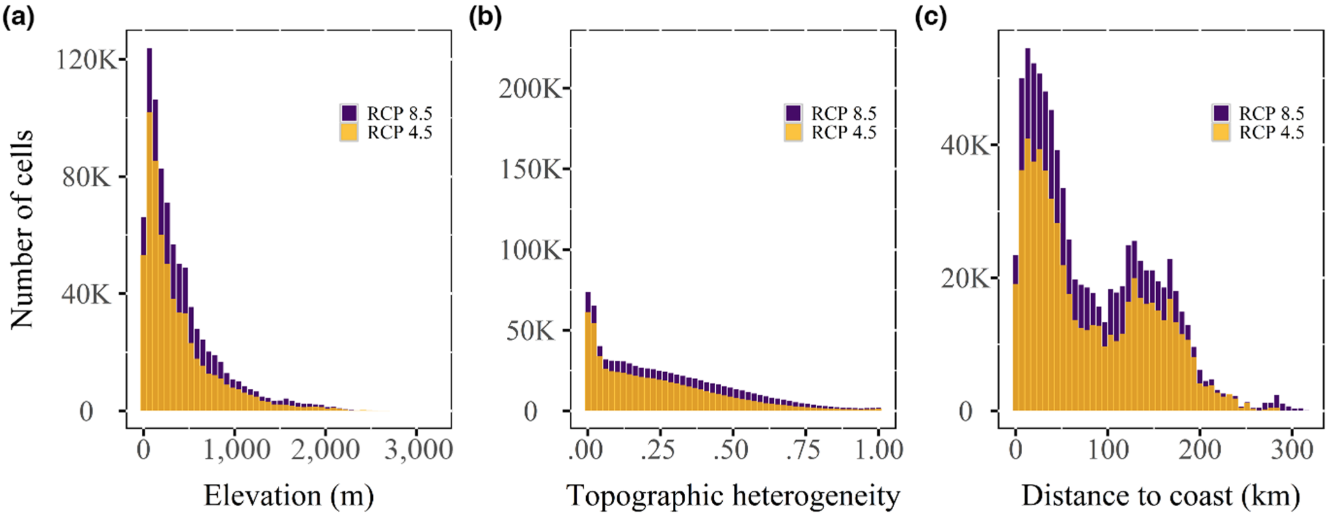

FIGURE 7 Frequency distribution of raster cells projected to become increasingly developed (natural to exurban/urban/agriculture or exurban to urban/agriculture) between 1995–2085 by elevation (m) (a), topographic heterogeneity (b) and distance to coast (km) (c) for emissions scenarios representative concentration pathway (RCP) 4.5 and RCP 8.5.

determining species' exposure to land use change, providing further evidence of the negative relationship between human impact and elevation that has been observed globally (Nogués-Bravo et al., 2008).

5 | CONCLUSIONS

Rarity and geographic traits are important determinants of species exposure to climate and land use change for plant species in the CFP. Our research highlights how complex interactions between these traits influence their exposure to global change and demonstrates the importance of analysing the relationship between species traits and vulnerability in multiple ways. While range size was an important predictor of species' exposure to global change for our study species, it interacted with other aspects of species' spatial distributions, including habitat configuration, elevation and topographic heterogeneity, to magnify or reduce species' vulnerability to habitat loss. Furthermore, we found that while species may be buffered from the consequences of one change driver, they may lose significant habitat under another, that is, species with many habitat patches are predicted to fare well under climate change but were among the most exposed to land use change. Overall, this research emphasizes the usefulness of traits derived from simple occurrence records and distribution models in predicting species exposure to future change and the importance of considering interactions between multiple traits in the context of climate and land use change.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA AVAILABILITY STATEMENT

The datasets and R script used in our final analyses relating exposure to species traits are included with our manuscript as Supporting Information. We included additional scripts used to build species distribution models, assess the impact of land use change, and calculate exposure in a GitHub repository (https://github.com/mrose048/sp_traits_exposure).

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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