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Impacts of 21st-century climate change on montane habitat in the Madrean Sky Island Archipelago

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Abstract

Aim: The Madrean Sky Island Archipelago is a North American biodiversity hotspot composed of ~60 isolated mountains that span the Cordilleran Gap between the Rocky Mountains and the Sierra Madre Occidental. Characterized by discrete patches of high-elevation montane habitat, these "sky islands" serve as stepping stones across a "sea" of desert scrub/grassland. Over this coming century, the region is expected to shift towards a warmer and drier climate. We used species distribution modelling to predict how the spatial distribution of montane habitat will be affected by climate change.

Location: Madrean Sky Island Archipelago, south-west United States and north-west Mexico (latitude, 29–34°N; longitude, 107–112°W).

Methods: To approximate the current distribution of montane habitat, we built species distribution models for five high-elevation species (*Ceanothus fendleri*, *Pinus strobiformis*, *Quercus gambelii*, *Sciurus aberti*, and *Synuchus dubius*). The resulting models were projected under multiple climate change scenarios—four greenhouse gas concentration trajectories (RCP 2.6, 4.5, 6.0, and 8.5) for each of three climate models (CCSM4, MPI-ESM-LR, and NorESM1-M)—to generate predicted distributions for the years 2050 and 2070. We performed chi-squared tests to detect any future changes to total montane habitat area, and Conover–Iman tests to evaluate isolation among the discrete montane habitat patches.

Results: While the climate models differ with respect to their predictions as to how severe the effects of future climate change will be, they all agree that by as early as year 2050, there will be significant montane habitat loss and increased montane habitat patch isolation across the Madrean Archipelago region under a worst-case climate change scenario (RCP 8.5).

Main conclusions: Our results suggest that under 21st-century climate change, the Madrean Sky Islands will become increasingly isolated due to montane habitat loss. This may affect their ability to serve as stepping stones and have negative implications for the region's biodiversity.

KEYWORDS

biodiversity hotspot, climate change, Madrean Sky Island Archipelago, montane habitat, species distribution modelling, stepping stones

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1 | INTRODUCTION

Human influences on Earth's climate system are unequivocal. Mean annual global surface temperatures increased ~0.85°C from 1880 to 2012 and are expected to rise by an additional 1–4°C by 2100; greater contrasts in annual mean precipitation between dry and wet regions, as well as larger contrasts between dry and wet seasons, are also anticipated by the end of this century (IPCC, 2013). The importance of broadscale temperature and precipitation conditions on where a species or a population can occur and persist (Grinnell, 1917; James, Johnston, Wamer, Niemi, & Boecklen, 1984; Whittaker, Levin, & Root, 1973) is especially relevant at the coarse geographic scale at which species distributions are typically defined (Soberón, 2007).

With anthropogenic climate change, a given species' current geographic range may no longer contain climatic conditions conducive to its survival. However, there are several ways in which species can potentially respond to climate change (e.g., Davis, Shaw, & Etterson, 2005; Holt, 1990). First, species may undergo plastic and/or evolutionary changes to adapt to the altered abiotic and/or biotic conditions within their existing geographic range. Second, species may track the original climatic conditions by dispersing over space (e.g., moving to higher latitudes or elevation as climates warm; Brusca et al., 2013; Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Parmesan & Yohe, 2003). Third, when neither adaptation nor dispersal is possible, the species may go extinct.

While there are multiple ways for species to potentially respond to climate change, the ability of species to adapt fast enough in-place to changing climatic conditions has been limited by the rapid rate of climate change. Already, there have been widespread local extinctions in hundreds of species across diverse climatic regions, habitats and taxonomic groups, particularly at the warm edge (i.e., lower latitudes and lower elevations) of their ranges (Wiens, 2016). This trend will inevitably continue as projected rates of future climate change are expected to outpace species' ability to adapt (Jezkova & Wiens, 2016).

For many species, the rate of climate change may exceed their adaptive capacities, but they can still contend with changing climatic conditions by dispersing over space (e.g., Chen et al., 2011). However, there are limits as to how far a given species will be able to track a shifting climate; in mountainous regions, climates already at the uppermost elevations can shift above mountain peaks and no longer be available for species to occupy (Colwell, Brehm, Cardelús, Gilman, & Longino, 2008; Nogués-Bravo, Araújo, Errea, & Martínez-Rica, 2007).

One such region that is at risk of having the availability of its high-elevation climates disappear under future climate change is the Madrean Sky Island Archipelago (Madrean Archipelago) of the south-western United States and north-western Mexico. Recognized as a biodiversity hotspot (Mittermeier et al., 2004), the Madrean Archipelago lies at a biogeographic crossroad (Spector, 2002) where its ~60 isolated mountains serve as "stepping stones" that span the Cordilleran Gap between the Rocky Mountains and the Sierra Madre Occidental. These "sky islands" are characterized by the elevational ordering of their distinct biological communities (i.e., biome-stacking; Marshall, 1957; Shreve, 1922), which include desert scrub, desert grassland, oak-grassland, oak woodland, chaparral, and—if elevations permit—pine-oak woodland, pine forest, and mixed conifer forest (Moore et al., 2013). Of the world's sky island complexes, the Madrean Archipelago is the only one to cross from temperate to subtropical latitudes and connect two major mountain systems (Rocky Mountains/Sierra Madre Occidental), as well as two floristic (Neotropic/Holarctic) and two faunal realms (Neotropic/Nearctic; Warshall, 1994).

The Madrean Archipelago's exceptional species richness and beta diversity are largely explained by its topography and relief, and its geographic location at the juncture of several ecologically distinct regions—the Rocky Mountains, Sierra Madre Occidental, and the Sonoran and Chihuahuan deserts. The rich set of climates and associated biomes supported by the Madrean Archipelago's topographically diverse landscape are home to a multitude of locally endemic species and have allowed many additional species to extend their ranges from adjacent regions. For several taxonomic groups, the Madrean Archipelago represents the biogeographic limit of their range. These include 30 bird species, over 35 reptile spp., and roughly 15 mammal spp., as well as 14 plant (northern limit) and 11 bird families (seven at their southern limit and four at their northern limit; Warshall, 1994). The convergence and overlap of all these species ranges have produced unrivalled levels of biodiversity. Over half of all bird species in North America occur in the Madrean Archipelago (Felger & Wilson, 1994), and it has the highest species richness for ants, mammals, and reptiles of anywhere on the continent (Warshall, 1994). The region is also likely to have the most diverse bee assemblage in the world (Buchmann, 1994).

Future climate change is expected to impact the Madrean Archipelago by causing an upward elevational shift of its climates and associated biomes (e.g., Colwell et al., 2008; Nogués-Bravo et al., 2007). As the uppermost biomes (i.e., pine forest and mixed conifer forest) retreat to higher elevations, these habitat "islands" will shrink and possibly disappear. The decrease in available habitat and the increase in "island" isolation may affect the region's overall biodiversity in the following ways. First, habitat loss and the effects of small patch size may lead to a greater likelihood of local extinctions (Andrén, 1994; Bender, Contreras, & Fahrig, 1998). Second, immigration may be important for sustaining local populations; within the Madrean Archipelago, increased "island" isolation may prevent some populations from receiving enough migrants to avoid local extinction (Hanski, 1998). If extirpated, their habitat patches may remain unoccupied for a greater duration before they are recolonized and new populations can become established (MacArthur & Wilson, 1967). Additionally, increased "island" isolation may prevent the "stepping stones" of the Madrean Archipelago from connecting the Rocky Mountains and Sierra Madre Occidental, functionally widening the Cordilleran Gap between the two mountain systems.

Here, we evaluate the effect of future climate change on the spatial distribution of high-elevation climates across the Madrean Archipelago. More specifically, we are interested in those climates that are suitable for species that occupy the uppermost biomes (i.e., pine forest and mixed conifer forest) exclusively. We will refer to those uppermost biomes collectively as the "montane" biome. We selected five species (three plants, one insect, and one mammal)

that are representative of the montane biome; within the Madrean Archipelago, they only occur at high elevations. For each species, we performed species distribution modelling to approximate the current distribution of montane habitat and projected the resulting models under multiple climate change scenarios—four greenhouse gas concentration trajectories (RCP 2.6, 4.5, 6.0, and 8.5) for each of three climate models (CCSM4, MPI-ESM-LR, and NorESM1-M)—to generate predicted distributions for the years 2050 and 2070. For each climate model under a worst-case future climate change scenario (RCP 8.5), (a) the proportion of the Madrean Archipelago consisting of the montane biome decreased significantly and (b) discrete patches of montane habitat became significantly more isolated from one another.

2 | METHODS

2.1 | Study area

The study area (Figure 1) is bounded by 29–34°N latitude and 107–112°W longitude and encompasses the roughly 230,000 km^2 Madrean Archipelago region of the south-west United States and north-west Mexico. This includes the entire complement of ~60 "Sky Islands" that span the Cordilleran Gap from the southern border of the Colorado Plateau to the north-western boundary of the Sierra Madre Occidental.

2.2 | Montane biome distribution modelling

To approximate the current spatial distribution of the montane biome across the Madrean Archipelago region and estimate the changes to that distribution under multiple future climate change scenarios, we performed species distribution modelling for five representative species under current climate conditions and future climate projections. Species distribution modelling is a process where environmental data associated with the geographic coordinates of species occurrence records and random background points (i.e., pseudo-absences) are evaluated by program-specific algorithms to assess habitat suitability across landscapes (Elith et al., 2006).

2.2.1 | Contemporary climate data

We obtained bioclimatic variables which had been derived from WorldClim v. 1.4 climate data (http://www.worldclim.org) at a 30 arc-second spatial resolution (~1 km; Table 1). WorldClim climate data are interpolated using ANUSPLIN (Hutchinson, 1995) to fit thin-plate smoothing splines through weather station data in three dimensions—latitude, longitude and elevation (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005). This method does have limitations; namely, its performance declines in regions where climates transition dramatically over short distances (e.g., the mountainous western United States; Daly et al., 2008). PRISM (http://prism.oregonstate.edu/) is an alternative climate dataset that outperforms WorldClim in mountainous regions (Daly et al., 2008). However, its spatial extent is limited to the United States. Because our study area included portions of the United States and Mexico, we selected WorldClim due to its global spatial extent. Additionally, future climate data are available through WorldClim and not PRISM. WorldClim has climate data representing two "current" time periods: 1960–1990 and 1970–2000. We selected climate data from the 1960–1990 time period since WorldClim's future climate data had been downscaled and calibrated to those data.

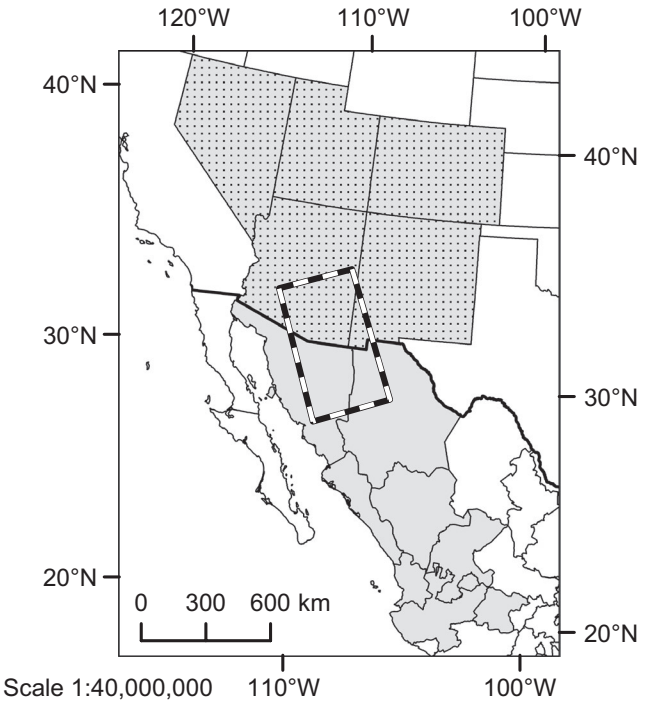


FIGURE 1 Map of the south-west United States and north-west Mexico. Species distribution models for *Ceanothus fendleri*, *Pinus strobiformis*, *Quercus gambelii*, *Sciurus aberti*, and *Synuchus dubius* were built using bioclimatic variables derived from contemporary WorldClim climate data clipped to the south-west United States (stippled). The resulting models were then projected onto the south-west United States and north-west Mexico (grey) using bioclimatic variables derived from contemporary and future climate data available from WorldClim. Landscape metrics (i.e., total montane habitat area and montane habitat patch proximity indices) were extracted from the Madrean Archipelago region (i.e., study area; hatched box). Map projection: US contiguous Albers equal-area conic

2.2.2 | Future climate data

We selected three climate models that were developed for the Coupled Model Intercomparison Project, phase 5 (CMIP5; Taylor, Stouffer, & Meehl, 2012): the Community Climate System Model v. 4 (CCSM4; Gent et al., 2011), the Max Planck Institute Earth System Model, low resolution (MPI-ESM-LR; Giorgetta et al., 2013), and the Norwegian Earth System Model v. 1, intermediate resolution (NorESM1-M; Bentsen et al., 2013). Over 50 climate models from 20 modelling groups participated in CMIP5; among those evaluated, there is considerable variation in their ability to replicate the continental and regional climatology of North America observed over

TABLE 1 List of data products used for species distribution modelling with their summary information according to their modelled years, representative concentration pathways (RCP), and reference

Data product	Years	RCPs (W/m^2)	Reference
WorldClim 30-year normals	1960–1990		Hijmans et al. (2005)
WorldClim CCSM4	2050, 2070	2.6, 4.5, 6.0, 8.5	Gent et al. (2011)
WorldClim MPI-ESM-LR	2050, 2070	2.6, 4.5, 8.5	Giorgetta et al. (2013)
WorldClim NorESM1-M	2050, 2070	2.6, 4.5, 6.0, 8.5	Bentsen et al. (2013)

Abbreviations: CCSM4, Community Climate System Model v. 4; MPI-ESM-LR, Max Planck Institute Earth System Model, low resolution; NorESM1-M, Norwegian Earth System Model v. 1; W/m^2, watts per square metre.

the past 30 years (Sheffield et al., 2013). While no single model outperformed the others across all climatic variables, there were some that consistently surpassed the rest for particular variables across most regions and seasons. We selected CCSM4, MPI-ESM-LR, and NorESM1-M for our study because they modelled western North America's climate (temperature and precipitation) for both winter (December, January, February) and summer (June, July, August) with the greatest accuracy (Sheffield et al., 2013).

CCSM4, MPI-ESM-LR, and NorESM1-M contributed to CMIP5 by predicting how Earth's climate will be impacted by a range of variables related to 21st-century population growth, technological development, energy and land use, socio-economic change, greenhouse gas emissions, and societal responses to climate change. These three models were projected under a set of four representative concentration pathways (RCPs; Moss et al., 2010; Van Vuuren et al., 2011). The RCPs are greenhouse gas concentration trajectories that summarize the anthropogenic factors that will lead to radiative forcing levels of 2.6, 4.5, 6.0, and 8.5 W/m^2 by the year 2100. We obtained bioclimatic variables for CCSM4, MPI-ESM-LR, and NorESM1-M for the years 2050 and 2070 under each RCP from the WorldClim v. 1.4 dataset at a 30 arc-second spatial resolution (Table 1).

2.2.3 | Bioclimatic variables

There are 19 bioclimatic variables, all derived from mean monthly precipitation and temperature (minimum and maximum) values (Nix, 1986). They collectively capture both annual conditions and intra-year seasonality—broad environmental trends that are biologically meaningful to the physiological constraints of a species. However, there is the potential for there to be multicollinearity among the variables (e.g., O'Donnell & Ignizio, 2012; Jezkova, Olah-Hemmings, & Riddle, 2011; Kozak & Wiens, 2006). To identify a subset of variables with minimal multicollinearity, we performed a reverse stepwise VIF (variance inflation factor) analysis with the package R.VIF (van Breugel, Friis, Demissew, Lillesø, & Kindt, 2016) in GRASS GIS v. 7.6 (GRASS Development Team, 2019). We evaluated the contemporary WorldClim climate data across the spatial extent of the south-west United States (Figure 1) using a VIF threshold of five after transforming the layers to a US contiguous Albers equal-area conic projection in order to minimize geographic distortions to area and distance. Seven bioclimatic variables were retained for species distribution modelling: mean diurnal range, temperature seasonality, mean temperatures of both the wettest and driest quarters, precipitation of both the wettest and driest months, and precipitation of the coldest quarter.

2.2.4 | Species locality data

Species locality data were acquired for five montane species (Table 2). These include three plant, one mammal, and one insect species whose ranges are predominantly at higher elevations (i.e., >1,800 m) within the south-west United States (i.e., Arizona, Colorado, Nevada, New Mexico, and Utah). Raw point locations, limited to the south-west United States, were obtained from SEINet (http://swbiodiversity.org/seinet/), VertNet (http://vertnet.org/), and the Symbiota Collections of Arthropods Network (SCAN; http://scan-bugs.org/portal/). Point locations for the insect, *Synuchus dubius*, were supplemented with personal collection records. Due to the under-representation of available species locality data from Mexico, we were limited to species found primarily within the United States.

The georeferenced localities were manually inspected for accuracy and updated when possible. Records whose precise locations could not be determined from their associated collecting/observation data were removed. This process was performed for *Synuchus dubius*; but because it was so time-intensive, an automated alternative was developed for the remaining species. Climate values were extracted for the species occurrences, and outlier records were identified with the R package CAR (Fox & Weisberg, 2011). Point locations that were outliers for at least five of the 19 bioclimatic variables were removed; subsequent investigation revealed their outlier status was nearly always the result of being incorrectly georeferenced. To reduce the effects of sampling bias, the point locations were spatially thinned with the R package SPTHIN (Aiello-Lammens, Boria, Radosavljevic, Vilela, & Anderson, 2019) so that all remaining points were at least 5 km from each other (see Figures S1.1–S1.5 in Appendix S1).

2.2.5 | Species distribution modelling

We performed species distribution modelling with MAXENT v. 3.3.3k (Phillips, Anderson, & Schapire, 2006; Phillips & Dudík, 2008), which uses the machine-learning technique of maximum entropy modelling to express a relative probability distribution that predicts the suitability of environmental conditions for a species across a defined geographic space (Phillips, Dudík, & Schapire, 2004). To determine the optimal MAXENT parameter settings for each of our five study species, we used the R package ENMEVAL (Muscarella et al., 2014) which executes a series of MAXENT models across a range of feature class combinations and regularization multipliers. It also provides a series

TABLE 2 List of species used for species distribution modelling with their summary information according to their classification, geographic range, elevational range (metres), the number of point locations used for model construction, and the point locations' data source and download date

Species	Common name	Order:Family	Geographic range	Elevation range (m)	Point locations (*n*)	Data source	Download date	References
Ceanothus fendleri (Gray, 1849)	Fendler's buckbrush	Rosales:Rhamnaceae	AZ, CO, NM, SD, TX, UT, WY; MEX: Chih., Coah., Son.	1,600–2,800	458	SEINet	23 August 2017	Christie et al. (2006)
Pinus strobiformis (Engelmann, 1848)	Southwestern white pine	Pinales:Pinaceae	AZ, NM, TX; northern MEX	1,900–3,000	133	SEINet	23 August 2017	Kral (1993)
Quercus gambelii (Nuttall, 1848)	Gambel oak	Fagales:Fagaceae	AZ, CO, NM, NV, OK, TX, UT, WY; MEX: Chih., Coah., Son.	1,000–3,030	1,052	SEINet	23 August 2017	Nixon (1997)
Sciurus aberti (Woodhouse, 1853)	Abert's squirrel	Rodentia:Sciuridae	AZ, CO, UT, WY; MEX: Chih., Dgo., Son.	1,700–2,600	292	VertNet	04 December 2017	Keith (1965), and Patton and Green (1970)
Synuchus dubius (LeConte, 1854)	Ground beetle	Coleoptera:Carabidae	AZ, CO, NM, NV, UT, TX	1,700–3,000	125	SCAN and personal records	11 December 2016	Lindroth (1956)

Abbreviations: AZ, Arizona; Chih., Chihuahua; Coah., Coahuila; CO, Colorado; Dgo., Durango; MEX, Mexico; NM, New Mexico; NV, Nevada; OK, Oklahoma; Son., Sonora; SD, South Dakota; TX, Texas; UT, Utah; WY, Wyoming.

of evaluation metrics for selecting the best model. We ran ENMEVAL using its default settings, 10,000 background points, and block data partitioning. Because the species point localities were limited to the south-west United States, north-west Mexico was excluded from model construction and calibration to avoid overfitting the models to conditions found near the point localities (e.g., Anderson & Raza, 2010). For each species, we selected the model with the lowest AICc and projected it onto the region encompassing the south-west United States and north-west Mexico (Figure 1) using the bioclimatic variables derived from the contemporary and future climate data available from WorldClim. Because the post-climate change environments onto which the models were projected were likely to contain novel climate conditions, projections were performed with "clamping". In MAXENT, "clamping" treats the values for environmental variables that lie outside the range of values used to train the model as being equally suitable/unsuitable as the training data's nearest bounding value.

While our species distribution models are able to predict the current and future distributions of suitable habitat for each of our five study species across the Madrean Archipelago region, they cannot guarantee a perfect correlation with each species' actual distribution. Our five study species are expected to have limited dispersal abilities. In plants (e.g, *Ceanothus fendleri*, *Pinus strobiformis*, and *Quercus gambelii*), seeds disperse short distances as a general rule (Cain, Milligan, & Strand, 2000; Willson, 1993) and long-distance seed dispersal events are rare (Nathan, 2006). The mammal species, *Sciurus aberti*, does not disperse between mountains (Keith, 1965), and *Synuchus dubius*, which is a flightless ground beetle (Lindroth, 1956), is not likely to either. Given these limited dispersal capacities and the topographic complexity of the Madrean Archipelago region, portions of the landscape where suitable habitat is present may simply be inaccessible to our species and therefore go unoccupied.

Even though our five species may not fully inhabit the montane habitat distributions predicted by the species distribution models, these species do belong to a higher-elevation montane community (e.g., Brusca et al., 2013; Meyer et al., 2015; Whittaker & Niering, 1964). The species composition of this montane community varies across the Madrean Archipelago region, but the biome itself is widely distributed (Felger & Wilson, 1994; Marshall, 1957). We make the assumption that the montane community, in one form or another, fully occupies our predicted montane habitat distributions.

2.3 | Statistical analyses

The MAXENT projections were output with a logistic format, which uses a continuous scale ranging from 0 to 1 to indicate the relative probability that suitable environmental conditions are present for a species across a defined geographic area (see Figures S1.1–S1.5 in Appendix S1). We converted each species' output projections to binary habitat suitability/unsuitability maps using their 10 percentile training presence logistic threshold. At this threshold, suitable habitat is defined to include 90% of the species point locality records used to develop the species distribution model. An omission rate of 10% was selected to reduce the influence of potential locality data errors (i.e.,

incorrectly georeferenced points) on the distribution of suitable habitat. The binary habitat maps were produced with scripts written for PYTHON v. 2.7 (https://www.python.org/) and implemented in ARCGIS DESKTOP v. 10.5.1 (ESRI, Redlands, California, USA). These scripts also extracted the following landscape metrics from the "study area" spatial extent (Figure 1): (a) total montane habitat area and the (b) surface area, perimeter, isolation index, and mean elevation of each montane habitat patch. Statistical analyses were performed with RSTUDIO v. 1.1.423 (RStudio Team, 2016) and R v. 3.4.3 (R Core Team, 2017).

2.3.1 | Total montane habitat area

The proportion of the Madrean Archipelago region classified as montane habitat for the current climate was compared against the proportion estimated for each of the future climate scenarios. Using habitat/non-habitat cell counts, we performed pairwise chi-squared tests of homogeneity (Pearson, 1900) with Holm corrections for multiple comparisons (Holm, 1979) using the R package FIFER (Fife, 2017). The pairwise comparisons were conducted within six discrete sets each composed of the present-day landscape modelled under the current climate, as well as the four predicted future landscapes (at the year 2050 or 2070) modelled by the same climate model (CCSM4, MPI-ESM-LR or NorESM1-M) under each of the four RCPs (2.6, 4.5, 6.0, and 8.5).

2.3.2 | Montane habitat patch metrics

We delineated the montane habitat patches across the binary maps by assigning every contiguous set of habitat cells (i.e., sharing an edge or diagonal) to a distinct group. For each montane habitat patch, we determined its proximity in relation to all other montane habitat patches across the landscape by calculating a proximity/isolation index (Gustafson & Parker, 1992; Whitcomb et al., 1981):

$$\text{Proximity Index} = \sum_{s=1}^{n} \frac{a_{ijs}}{h_{ijs}^2}$$

where n is the number of habitat patches, a_{ijs} is the area (m^2) of patch *ijs*, and h_{ijs} is the Euclidean distance (m) between patch *ijs* and patch *ijs* based on patch edge-to-edge distance. A patch's proximity index value is found by dividing the area of a second patch (patch *j*) by the square of the nearest edge-to-edge distance between the two patches and taking the sum from every comparison to the first patch (patch *i*; McGarigal, 2015). Lower proximity index values indicate greater isolation.

Given the topographic complexity of the Madrean Archipelago region, we computed each patch's surface area rather than its planimetric area. Surface areas were derived with methods developed by Jenness (2004) using 30 arc-second DEMs (digital elevation models) obtained from the SRTM30 v. 2.1 dataset (Shuttle Radar Topography Mission; https://dds.cr.usgs.gov/srtm/version2_1/SRTM30/). Also, to ensure that the Euclidean inter-patch distances were between edges rather than cell centres, we converted the patches (i.e., sets of contiguous habitat cells) to polygons. Additionally, the 30 arc-second DEMs were used to derive the mean elevation of each montane habitat patch.

Using base-10 log-transformed proximity index values, we performed Conover–Iman pairwise tests for multiple comparisons of mean rank sums (Conover & Iman, 1979) with Holm corrections for multiple comparisons (Holm, 1979) using the R package PMCMR (Pohlert, 2014). The pairwise comparisons were conducted within the same sets of landscapes that we used for the total montane habitat area pairwise comparisons. We repeated the analysis using base-10 log-transformed surface areas, base-10 log-transformed perimeters, perimeter/area ratios, and the mean elevations of the habitat patches.

3 | RESULTS

3.1 | Species distribution models

The ENMEVAL analyses evaluated 48 MAXENT models for each species to identify the optimal combination of feature classes and regularization multipliers. Each species' best species distribution model (i.e., lowest AICc) included every available feature class (linear, quadratic, hinge, product, and threshold), except for *P. strobiformis* which included all but the threshold feature class. The regularization multipliers for the best models were 4, 4, 1, 3.5, and 3 for *C. fendleri*, *P. strobiformis*, *Q. gambelii*, *Sciurus aberti*, and *Synuchus dubius*, respectively. The area under the receiver operating characteristic (ROC) curve (AUC) is a metric for evaluating classification accuracy in species distribution models. The mean AUC values for the best models were 0.885 ± 0.070, 0.954 ± 0.018, 0.842 ± 0.021, 0.889 ± 0.051, and 0.911 ± 0.063 for *C. fendleri*, *P. strobiformis*, *Q. gambelii*, *Sciurus aberti*, and *Synuchus dubius*, respectively (See Figure S2.6 in Appendix S2). AUC values range from 0.5 for a random prediction to 1 for a perfect prediction (Fielding & Bell, 1997). These models capture well the present-day distribution of montane biome habitat and illustrate how the Madrean Archipelago region is composed of "sky island stepping stones" that span the Cordilleran Gap from the southern border of the Colorado Plateau to the northwestern boundary of the Sierra Madre Occidental (see Figures S1.1–S1.5 in Appendix S1).

3.2 | Total montane habitat area

Estimates of potential montane habitat loss across the Madrean Archipelago region by the year 2050 range from nearly 50% for *C. fendleri*, *P. strobiformis*, *Q. gambelii*, and *Synuchus dubius* to as high as 70% for *Sciurus aberti* under a worst-case climate change scenario (RCP 8.5; Figures 2 and 3a). These same losses are dramatically reduced under a best-case climate change scenario (RCP 2.6) with estimated losses ranging from 40% for *Sciurus aberti* to as low as 15% for *Q. gambelii* and *Synuchus dubius*, and even 7% for *C. fendleri* and *P. strobiformis* (Figures 2 and 3a). A similar, but more pronounced, trend of RCP 8.5 montane habitat loss was seen for the MPI-ESM-LR and NorESM1-M climate models (see Figures S3.7–S3.11 in Appendix S3 and Figures S4.12a–S4.13a in Appendix S4). However,

the reductions to montane habitat loss under RCP 2.6 were not as great as those seen for the CCSM4 climate model.

3.3 | Montane habitat patch surface area, perimeter, and perimeter/area ratio

We were unable to detect any statistically significant changes to the mean surface area, perimeter, or perimeter/area ratio of the montane habitat patches between the current and future landscapes for any of the species. This result was unexpected, and we provide the following explanation for this pattern. The current landscapes had an overwhelming number of very small habitat patches that were making an outsized contribution to the mean value of the patch metrics. These small habitat patches tended to be in close proximity to much larger habitat patches corresponding to mountain ranges. For the future landscapes, the small habitat patches from the current landscape disappeared and the larger habitat patches shrunk, as expected. But as the larger habitat patches shrunk, their edges fragmented into small habitat patches that replaced those that were lost. Ultimately, there were still an overwhelming number of very small habitat patches that kept the mean values of the patch metrics for the future landscapes from being any different from those of the current landscapes.

3.4 | Montane habitat patch isolation

The discrete patches of montane habitat across the Madrean Archipelago region are expected to become more isolated by the year 2050 under RCP 8.5 (Figures 2 and 3b). This is driven by shrinking patch sizes. However, RCP 2.6 is expected to prevent this trend and keep habitat patches from becoming more isolated by the year 2050 (Figures 2 and 3b). For the MPI-ESM-LR and NorESM1-M climate models, montane patch isolation by the year 2050 under RCP 8.5 is more severe than for CCSM4 and RCP 2.6 is unable to prevent habitat patches from becoming more

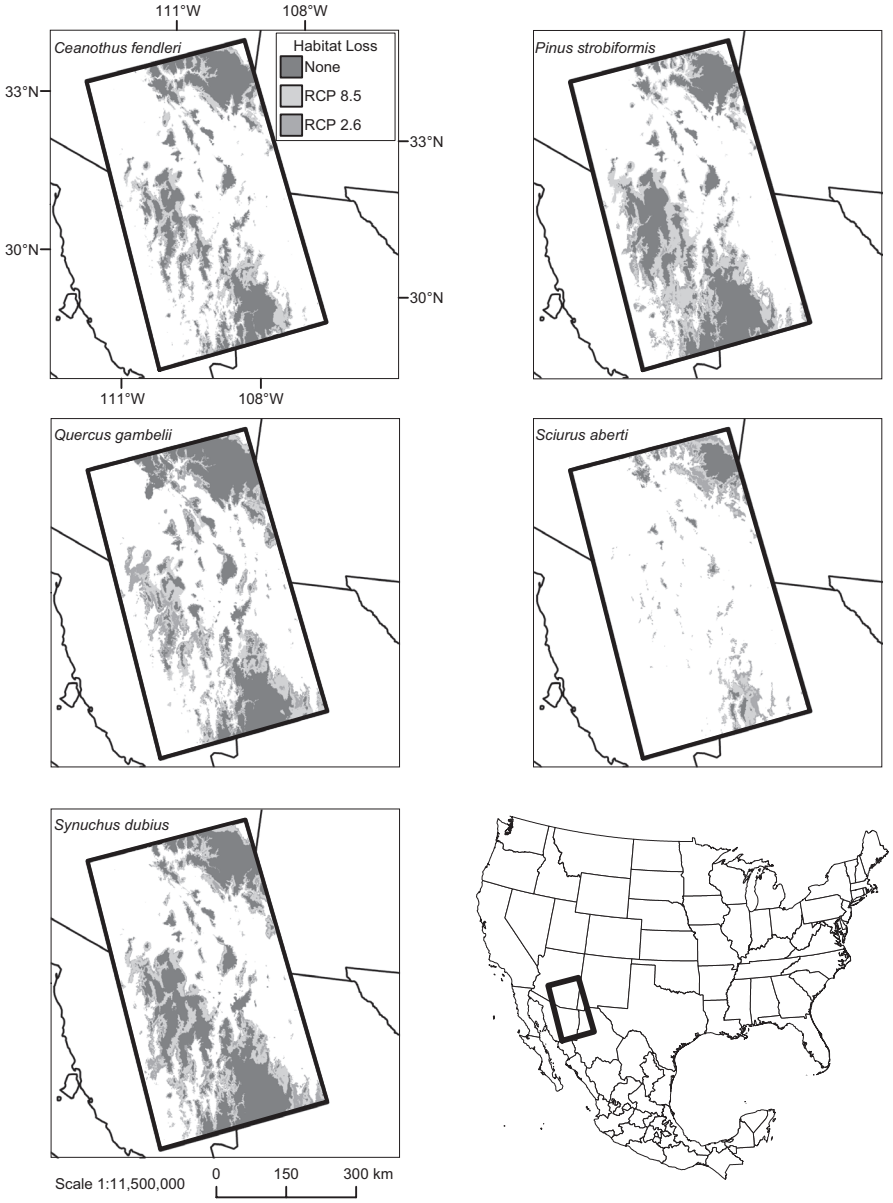


FIGURE 2 Predicted Madrean Archipelago montane habitat loss (present—2050) based on species distribution models for *Ceanothus fendleri*, *Pinus strobiformis*, *Quercus gambelii*, *Sciurus aberti*, and *Synuchus dubius* projected under the Community Climate System Model v. 4 (CCSM4). Maps represent the distributions of montane habitat at present (light, medium, and dark grey collectively) and at the year 2050 under representative concentration pathways (RCPs) of 2.6 (light and dark grey collectively) and 8.5 W/m^2 (dark grey). Associated montane habitat losses under RCP 2.6 (medium grey) and 8.5 (light and medium grey collectively) are for a best- and worst-case future climate change scenario, respectively. Note: each species' three montane habitat distributions are nested (RCP 8.5 within RCP 2.6, and both within present) except for *Q. gambelii* where there is a slight expansion at the north-central most portion of the Madrean Archipelago region under RCP 2.6 and 8.5 compared with present. Map projection: US contiguous Albers equal-area conic

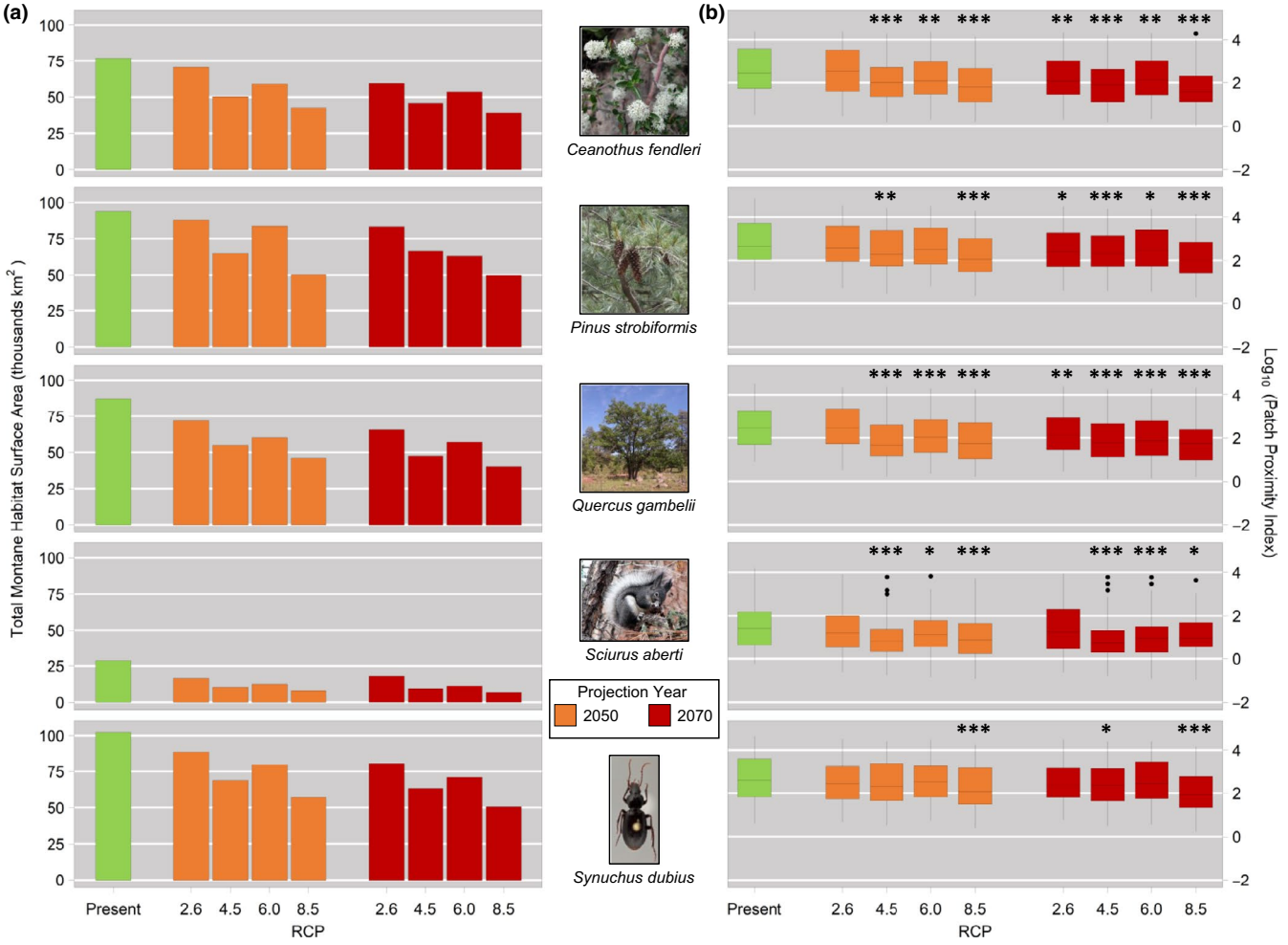


FIGURE 3 (a) Total montane habitat surface area (thousands kilometres^2) for the Madrean Archipelago region by species, projection year, and representative concentration pathway (RCP). Future climate projections were performed under the Community Climate System Model v. 4 (CCSM4). The surface area for every future climate projection is significantly less than the present-day surface area based on Holm-corrected chi-squared pairwise comparisons among RCPs grouped by projection year ($p < 0.001$). (b) Log-transformed montane habitat patch proximity index values for the Madrean Archipelago region by species, projection year, and RCP. Future climate projections were performed under the Community Climate System Model v. 4 (CCSM4). Holm-corrected probabilities based on Conover–Iman pairwise comparisons among RCPs grouped by projection year are shown with asterisks and indicate future landscapes whose montane habitat patches are significantly more isolated from each other than those for the present day. *Significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$. Photo credits: Max Licher (*Ceanothus fendleri*, *Pinus strobiformis*, *Quercus gambelii*); US National Park Service (*Sciurus aberti*); Chip Hedgcock (*Synuchus dubius*)

isolated, but it is able to reduce the degree of patch isolation that would otherwise be seen under RCP 8.5 (see Figures S3.7–S3.11 in Appendix S3 and Figures S4.12b–S4.13b in Appendix S4).

3.5 | Montane habitat patch elevation

The mean elevation of montane habitat patches across the Madrean Archipelago region has the potential to increase anywhere from 150 m for *C. fendleri* and *Sciurus aberti* to as much as 300 m for *P. strobiformis* and *Q. gambelii* by the year 2050 under RCP 8.5 (Figure 4). However, RCP 2.6 is expected to reduce the degree to which mean elevations rise, and in some instances, prevent that rise entirely (Figure 4). The MPI-ESM-LR and NorESM1-M climate models predict an even greater rise in mean elevation by 2050 under RCP 8.5. However, RCP 2.6 is unable to reduce the elevational rise to the same degree as for the CCSM4 climate model (see Figures S5.14–S5.15 in Appendix S5).

4 | DISCUSSION

In this study, we evaluated the impact of future climate change on the spatial distribution of high-elevation montane habitat across the Madrean Archipelago region based on species distribution modelling for five montane species (*C. fendleri*, *P. strobiformis*, *Q. gambelii*, *Sciurus aberti*, and *Synuchus dubius*). The species' current habitat distributions are composed of discrete patches, which highlight the "stepping stones" that characterize the Madrean Archipelago region

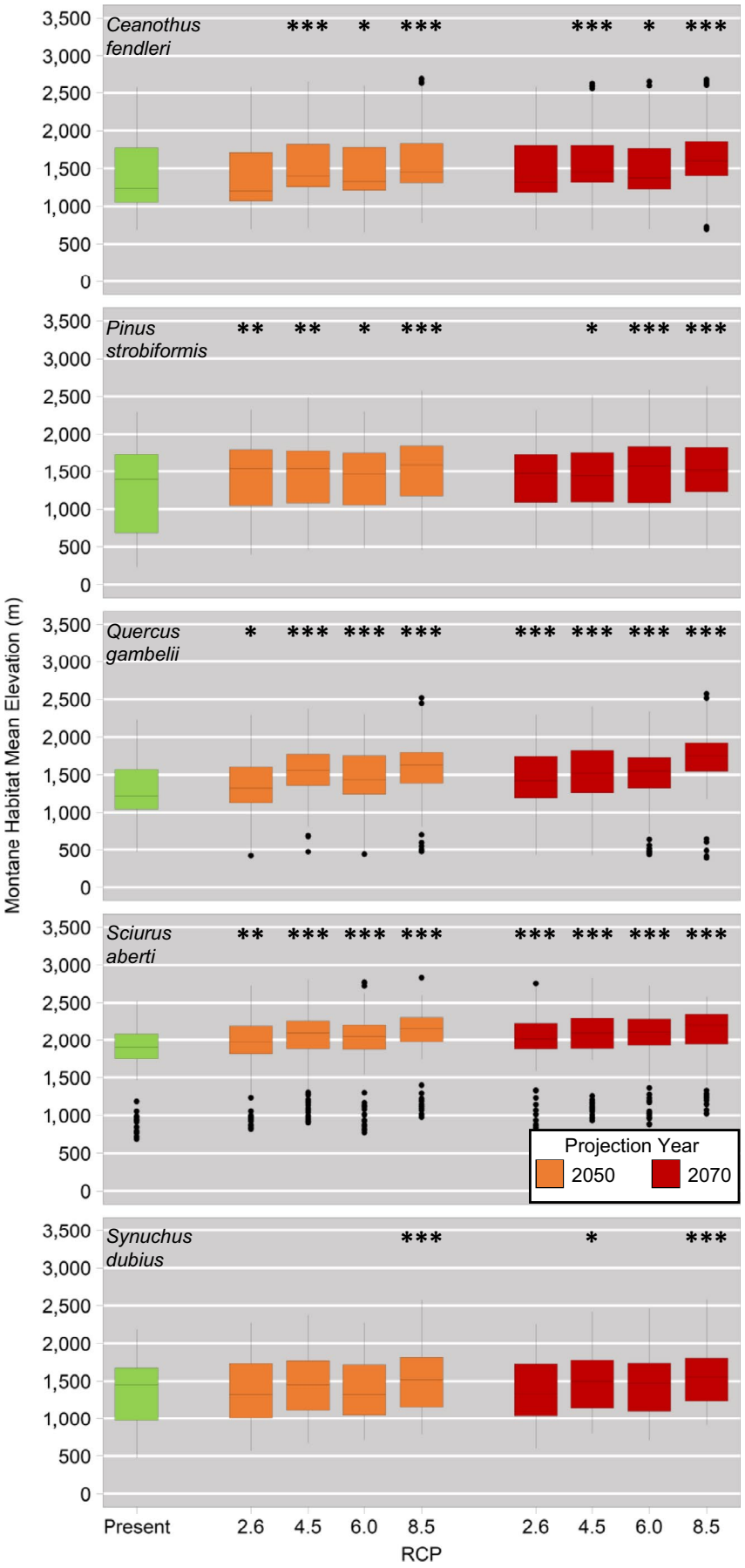


FIGURE 4 Montane habitat mean elevation in metres for the Madrean Archipelago region by species, projection year, and representative concentration pathway (RCP). Future climate projections were performed under the Community Climate System Model v. 4 (CCSM4). Holm-corrected probabilities based on Conover–Iman pairwise comparisons among RCPs grouped by projection year are shown with asterisks and indicate future landscapes whose montane habitat patches are at significantly higher elevations than those for the present day. *Significant at $p < 0.05$; **significant at $p < 0.01$; ***significant at $p < 0.001$

(Figure 2). Under a worst-case future climate change scenario (RCP 8.5), these "stepping stones" will become more isolated from one another (Figure 3b) as montane habitat shifts in elevation (Figure 4) and is lost (Figure 3a). While the three independent climate models used in this study differ with respect to their predictions as to how severe the effects of future climate change will be, they all agree that by as early as year 2050, there will be significant montane habitat loss and increased montane habitat patch isolation across the Madrean Archipelago region under a worst-case future climate change scenario.

The montane habitat in the Madrean Archipelago region contains a unique community of species (e.g., Brusca et al., 2013; Meyer et al., 2015; Whittaker & Niering, 1964). Montane habitat loss and the increased isolation of montane habitat patches under future climate change will likely threaten the biological diversity of the Madrean Archipelago region, particularly through their effects on these montane populations. Habitat loss can cause population sizes to decline; in landscapes where habitat is already highly fragmented (e.g., Madrean Archipelago region), shrinking patches and increasing isolation can amplify the trend and lead to even greater declines than would be expected from pure habitat loss alone (Andrén, 1994). As patches shrink, their proportion of habitat edge will increase, which can be especially detrimental to species associated with the habitat's interior (Bender et al., 1998) where biotic and abiotic conditions can differ dramatically from that of the edge (Murcia, 1995).

When population numbers decline in response to factors such as habitat loss and shrinking patch sizes, their genetic variation declines as well (Frankham, 1996). This can be through genetic drift, a process whereby allele frequencies randomly fluctuate from one generation to the next due to chance. In large populations, these fluctuations are mostly minor; but in small populations, they can be so great as to cause the fixation or loss of an allele (Hedrick, 2011). Additionally, the deleterious effects of inbreeding depression on population fitness (Charlesworth & Charlesworth, 1987) can become more likely in small populations (Ellstrand & Elam, 1993). The combined effects of genetic drift and inbreeding depression can ultimately reduce the ability of small populations to withstand environmental change and increase their susceptibility to extinction (Frankham, 2005; Reed & Frankham, 2003).

Gene flow can counteract the effects of genetic drift and inbreeding depression by replenishing genetic variation and boosting population fitness, thereby increasing the potential for populations to persist (Ingvarsson, 2001; Tallmon, Luikart, & Waples, 2004; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015). For populations to benefit from gene flow, individuals must be able to disperse between them. This is already a difficult endeavour for montane species in the Madrean Archipelago region, where desert scrub/grassland can prevent movement between "sky islands" (e.g., Holycross & Douglas, 2007; Lamb, Jones, & Wettstein, 1997; Mitchell & Ober, 2013; Sullivan, 1994; Tennessen & Zamudio, 2008). Under future climate change, environmental conditions at those lower elevations are expected to become even less hospitable to montane species, which will make the non-habitat "matrix" an even more formidable dispersal barrier. Additionally, dispersal will become an even greater challenge due to the increased isolation of montane habitat patches (Figure 3b). As the distance from a source patch increases and the size of the target patch decreases, individuals must travel further to reach a smaller destination, leading to a decline in successful dispersal events (Lomolino, Brown, & Sax, 2010; MacArthur & Wilson, 1967). Without dispersing individuals to provide additional genetic variation to montane populations suffering from the effects of genetic drift and inbreeding depression, there will be a greater risk of those populations going extinct.

Montane populations will be further imperilled when set against a landscape where the severity of ecological disturbances (e.g., droughts, insect outbreaks, and wildfires) is expected to rise (Dale et al., 2001). Over this next century, the climate of the Madrean Archipelago region is projected to shift towards greater aridity (Seager et al., 2007; Seager & Vecchi, 2010) where precipitation shortages lead to a marked increase in the number and duration of extreme dry events (i.e., droughts) that are exacerbated by less snowpack, warmer summer temperatures, and diminished runoff and soil moisture (Cayan et al., 2010). Droughts represent a serious threat to the forests that compose the montane habitat patches. Under protracted water stress, tree mortality can result from permanent cavitation of water columns within the xylem, and from carbon starvation as trees try to limit water loss through stomatal closure, constraining photosynthesis (McDowell et al., 2008). Across the western United States, warming temperatures and increasing water deficits have contributed to widespread tree mortality (Allen et al., 2010; van Mantgem et al., 2009); for the south-western United States, this trend is expected to accelerate (Williams et al., 2010). An additional consequence of water stress is that it weakens tree defences against attack from insects such as bark beetles (Raffa et al., 2008; Raffa, Aukema, Erbilgin, Klepzig, & Wallin, 2005), which have caused extensive forest losses across the south-western United States (Williams et al., 2010). Warming temperatures can potentially reduce bark beetle development times and enhance winter survival leading to a greater risk of population outbreaks and increased tree mortality within the region (Bentz et al., 2010). Also, bark beetle damage can add to existing fuel loads (i.e., dead trees) from droughts to further promote future wildfires (Dale et al., 2001). For the south-west United States, a large portion of its forests have already been affected by wildfires (Williams et al., 2010), whose severity is expected to rise as the region transitions to a warmer and drier climate (Brown, Hall, & Westerling, 2004). The significance of wildfires to the Madrean Archipelago region stems from their potential to cause sharp reductions in population sizes (i.e., population bottlenecks). Any resulting losses of genetic diversity and reductions in expected heterozygosity will be particularly difficult for populations to recover from when immigration rates are low (Banks et al., 2013). Given that the montane habitat patches will become increasingly isolated from one another under future climate change (Figure 3b), the effects of wildfire on their populations may be especially devastating.

To conclude, our study is not without its limitations, especially regarding spatial scale. We used climate data that had a spatial resolution of ~1 km, which is relatively coarse for mountainous regions, and can cause habitat loss to be overestimated (Engler et al., 2011). Also, a ~1 km spatial scale is unable to realistically capture the topographic complexity of the Madrean Archipelago region, which means

microrefugia go undetected (Mosblech, Bush, & van Woesik, 2011). Microrefugia can serve an important role as areas where populations can contract and persist for prolonged periods of time (e.g., Patsiou, Conti, Zimmerman, Theodoridis, & Randin, 2014); by their being under-represented, we overestimate both the degree of isolation that populations in the Madrean Archipelago region may face and their extirpation risk. Finally, we used "current" climate data representative of the years 1960–1990, so it is likely that our estimates of habitat loss include losses that have occurred prior to the present day.

Despite those limitations, our results still suggest that 21st-century climate change will have a significant impact on the availability of montane habitat within the Madrean Sky Island Archipelago. As habitat area is lost, population sizes may decline, leading to losses in genetic diversity and population fitness. Similar effects can result, albeit more suddenly, from ecological disturbances such as wildfires, which may become increasingly severe under climate change. We expect that the ability for populations to maintain/recover their genetic diversity via dispersal will diminish as montane habitat patches become more isolated from one another. Ultimately, the "sky islands" may lose their capacity to serve as functional "stepping stones," and an important factor contributing to the status of the Madrean Sky Island Archipelago as a biodiversity hotspot will disappear. However, if efforts are taken to mitigate climate change and a best-case scenario (RCP 2.6) can be achieved, montane habitat losses can be dampened (Figure 3a) and increases to patch isolation may even be prevented (Figure 3b).

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

DATA ACCESSIBILITY

Bioclimatic layers used for species distribution modelling are publicly available at https://www.worldclim.org. Occurrence records for all modelled species are publicly available through the following web-based museum collections databases: https://scan-bugs.org/portal, http://swbiodiversity.org/seinet/index.php, and http://vertnet.org. DEMs used for calculating surface areas are publicly available at https://dds.cr.usgs.gov/srtm/version2_1/SRTM30.

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BIOSKETCHES

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Author contributions: A.D.Y. designed the study with input from W.M.; A.D.Y. gathered and analysed the data; and A.D.Y wrote the manuscript with helpful comments from W.M.

SUPPORTING INFORMATION

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

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