

Climate Refugia for Pinus Spp. In Topographic and Bioclimatic Environments of the Madrean Sky Islands of México and the United States

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Research Article

Keywords: Madrean sky islands, climate change, conservation, microrefugia, Pinus spp., remote sensing indices

Posted Date: April 12th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-391708/v1>

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Version of Record: A version of this preprint was published at Plant Ecology on April 1st, 2022. See the published version at <https://doi.org/10.1007/s11258-022-01233-w>.

Abstract

Context

Refugia are island-like habitats that are linked to environmental stability. Where topography acts as a deterministic control, microrefugia may continue to function as habitat under reduced rates of climate change. Continental island ecosystems provide propitious settings for identifying patterns of refugia at multiple scales and applying that knowledge to conservation.

Objectives

Our main objective was to identify microrefugia for pines where habitats are defined by topographic heterogeneity. Secondary aims were to describe climatic variation within microrefugia and examine how species' response to seasonal climate alters spatial predictions of microrefugia.

Methods

We investigated how topography forms microrefugia in the Madrean sky islands, located in the borderlands of México and the United States. Our design incorporated pine species presence and absence field observations (*P. strobiformis*, *P. engelmannii* and *P. chihuahuana*, *P. arizonica* and *P. discolor*), modeled in relation to terrain, bioclimatic and remote sensing predictors.

Results

Terrain ruggedness, slope position and aspect defined microrefugia for pines within specific elevation ranges. Some species had narrow habitat preferences (e.g., *P. chihuahuana*); others exhibited a broader range of tolerance (e.g., *P. arizonica*). Hotspots of microrefugia were either limited to northern islands or occurred across central or southern latitudes. Response to seasonal climates shifted distributions of hotspots for species with open canopy structure and where regular fires occur.

Conclusions

Pine habitats with greater climate stability may provide holdouts and stepping-stones critical to species persistence with future change. Networks of refugia provide a promising focus for conservation, restoration, and fire management across a diverse, binational region.

Introduction

The ability of refugia to facilitate species persistence under adverse conditions of the past signals their potential importance in protecting biodiversity with future change. Refugia are island-like habitats that are linked to long-term environmental stability (Keppel et al. 2018) and can be identified at broad spatial and temporal scales (Ashcroft 2010; Morelli et al. 2020). Within broadly favorable climates, microrefugia defined by topographic heterogeneity can facilitate species persistence outside their physiological limits by modification of regional climate (Boyko 1947; Dobrowski 2011; Hampe and Jump 2011; Keppel et al. 2012). Where topography acts as a deterministic control on the geographical distribution of microrefugia, these places may continue to function as habitat under reduced rates of climate change (Mackey et al. 2012; Morelli et al. 2016). Furthermore, disturbances result in the formation of refugia where locations that are disturbed less severely or frequently than the

surrounding landscape harbor biological legacies that contribute to ecosystem recovery (Krawchuk et al. 2016; Haire et al. 2017; Krawchuk et al. 2020). An important strategy for conservation is to identify refugia that exist within high priority landscapes (Lawler 2009).

Continental island ecosystems, or sky islands, provide propitious settings for identifying macro- and microrefugia and applying that knowledge to conservation. The isolation of mountain islands coupled with high climatic variation that characterize sky islands are key components of macrorefugia where the evolution and persistence of unique species and communities are supported at multiple scales (Hampe and Jump 2011; Ashcroft et al. 2012; Morelli et al. 2020). The configuration of mountain complexes, their origins and geology, and the presence of bridges and barriers to movement promote high species richness and endemism along topographic gradients (Warshall 1995). Topographically driven isolation increases species diversification across elevation, with greater effects at lower latitudes (Steinbauer et al. 2016). Sky island ecosystems occur across the globe: the Himalaya-Hengduan Mountains in southwest China (Luo et al. 2016); the Western Ghats in India (Krishnadas and Osuri 2020; Jins et al. 2021); and the sky islands of eastern Africa (Popp et al. 2008).

Important insights for biodiversity and conservation with forecasted climate change have emerged from studies of tepuis, the flat-topped table mountains of the Guayana Highlands in South America (Vegas-Vilarrúbia et al. 2012; Nogué et al. 2013; Safont et al. 2016). Climate refugia were identified at broad scales where tepuis mountain species, adapted to a limited range of environmental conditions, concentrated in remaining habitat patches (Vegas-Vilarrúbia et al., 2012). Evidence from sky islands of the Guayana Highlands indicate that identifying potential refugia at regional scales can provide critical information for in situ conservation strategies in mountain environments (Scherrer and Körner 2011). However, complementary understanding of microrefugia that may increase the probability of species persistence at finer scales is needed (Vegas-Vilarrúbia et al. 2012).

Here, we investigate the potential for refugia to promote conservation in the Madrean sky islands, located in the borderlands of México and the United States. The Madrean sky islands are a stepping-stone archipelago comprised of montane habitats separated by lowland grassland, desert scrub and subtropical thornscrub and occur across steep and complex topography (Coblentz and Riiter 2004; Coblentz 2005). The region is a widely recognized biodiversity hotspot owing to its unique geography, specifically, the convergence of temperate and subtropical biomes between two cordilleras, the Rocky Mountains, and Sierra Madre Occidental (Warshall 1995; Spector 2002; Mittermeier et al. 2004). The north-south configuration of these sky islands likely contributed to dispersal in the past, increasing biodiversity with fluctuating climates. Advancing and receding montane vegetation dominated by pines (*Pinus* spp.) and oaks (*Quercus* spp.) drove vicariance and speciation, with movement fostered by low elevation passes between the two cordilleras and connectivity between the Chihuahuan and Sonoran deserts (Findley 1996).

Pines are an integral part of the diverse forests and woodlands that underpin ecological functions across the Madrean sky islands and are under extreme risk from habitat loss and increased isolation due to climate change and wildfire (Barton and Poulos 2018; Shirk et al. 2018; Yanahan and Moore 2019). Many species of pines in the region occur at the margins of their distributions (Ferguson et al. 2013), increasing vulnerability to stressors including drought stress, disturbance, and limits to dispersal ability (Hampe and Petit 2005). Identification of pine refugia can provide a focus for conservation efforts for these keystone species as they exist within a wide range of communities across their distributions.

Within the Madrean sky islands, pines occur in higher elevation forests with spruce-fir (*Picea engelmannii*-*Abies concolor*) and mixed conifer species (e.g., *Abies concolor*, *Populus tremuloides*, *Pseudotsuga menziesii*) primarily on northern islands (Rehfeldt et al. 2012; Villarreal et al. 2020). At lower latitudes and elevations, pine-oak forests include a mixture of species including *P. arizonica*, *P. engelmannii* and *Quercus* spp. Pines form a lesser component of evergreen forests and woodlands where oaks (*Quercus* spp.) are predominant. Pinyon-juniper (*P. edulis*, *P. discolor*, *Juniperus* spp.) woodlands are common across middle to lower elevations and latitudes. Notably, Madrean pine-oak woodlands of the southwestern United States and México comprise one of the 36 global biodiversity hotspots endangered by climate change and human impacts (González-Elizondo et al 2012; Conservation International 2020).

Resilience of pine forests and woodlands to climatic change is also influenced by land-use practices and variation in environmental stewardship and management. The bi-national Madrean sky island region is culturally and economically diverse, and a wide range of land uses, jurisdictions and management goals create environmental pressures (Villarreal et al. 2019a). Urban and exurban growth on both sides of the United States-México border, as well as vegetation clearing for border wall construction are reducing habitat area, quality, and connectivity for a wide range of species (Flesch et al. 2010; Villarreal et al. 2013; Peters et al. 2018). Activities that prevent or encourage burning, combined with warmer drier climates, can alter fire regimes in ways that reduce fire-free intervals and limit forest recovery (Iniguez et al. 2016; Villarreal et al. 2020). Cooperative efforts between conservation groups and public-private partnerships can help harness scientific resources and address pressing conservation issues exacerbated by climate change in this transboundary region (Aburto-Oropeza et al. 2018; Villarreal et al. 2019a; Norman 2020). However, conservation planning in the Madrean sky islands has been hindered by the lack of high quality and consistent transboundary data sets (Pezzoli et al. 2014).

In this study, we developed multi-scale species distribution models to identify and characterize refugia for pine species across the Madrean sky islands. The models serve to identify locations that function as microrefugia at fine scales where climatic change is expected to proceed more slowly due to heterogeneity in mountain topography (Hannah et al. 2015; Morelli et al. 2020). We then determined the range of variability in climate parameters associated with microrefugia, based on broader scale bioclimatic data. Last, we examined the variability in species response to seasonal climate to capture heterogeneity in species composition across forests and woodlands, and thus provide a perspective on shifts in microrefugia with current conditions.

Methods

Study region

The 74,788 km² Madrean Archipelago Ecoregion (Omernik 1987), or Madrean sky islands, encompasses portions of the northern states of Sonora and Chihuahua in México, and southeastern Arizona and southwestern New Mexico in the United States (Fig. 1). Our study included 55 sky island mountain complexes within the ecoregion, with an area of approximately 45,000 km² (Deyo et al. 2013). The international border divides the ecoregion near the center at 31°33 N.

The parallel valley and mountain configuration of the Madrean sky islands resulted from continental-scale deformation over the past several hundred million years in response to plate tectonics (Coblentz 2005). Valleys receded to expose older rocks derived from marine invasions, caldera eruptions and lava flows and metamorphic

core complexes (Warshall 1995). Mountain ranges are surrounded by temperate desert grassland and both temperate and subtropical scrub communities formed at the junction of the Sonoran and Chihuahuan deserts.

Climate in the region is characterized by a bimodal precipitation pattern. Winter (November to March) frontal storms bring snow to higher elevations and rain to the lower elevations (Adams and Comrie 1997; Sheppard et al. 2002). In mid- to late-summer (July to August), moisture from the south creates a monsoonal weather pattern with thunderstorms. The arid foresummer period (April to June) preceding the monsoonal moisture is typically hot and dry and generally corresponds to the fire season. Annual precipitation varies greatly by elevation, with orographic uplift contributing to increased precipitation at upper elevations.

Pine species descriptions

The five pine species vary in their association with particular environments (Table 1). Many studies reported relative affinities based on comparisons with other species, limiting interpretations of absolute limits or preferences. However, reports of broad environmental tolerance suggest that diverse microclimates associated with topographic variability could be utilized by species including *P. strobiformis*. Likewise, reports of drought tolerance suggest that cooler and wetter microclimates (e.g., mesic, north-facing slopes inhabited by *P. arizonica*) may provide refugia to some degree as warmer and drier regional climates affect local conditions. For *P. discolor*, tolerance of cooler, more mesic conditions at higher elevations could accommodate upward migration, while drought resistance could promote survival in its current range. Sensitivity of *P. engelmannii* to drought severity could make microrefugia that are decoupled from regional climate especially important to this species. Although *P. chihuahuana* has shown potential to adapt to warmer temperature, poor soils and wildfire, conditions conducive to regeneration may benefit from sheltered habitats found in microrefugia.

Table 1. Affinities of the five pine species with the climatic environment, documented in recent literature. Geographic focus refers to data sources from Northern (mostly United States); Southern (primarily México) and Region-wide (sky islands and beyond). English and Spanish common names were reported in Felger et al. (2001, and verified by M.S. Gonzalez-Elizondo, pers. comm.). For some species, scientific names represent groupings of synonyms from Plants of the World Online (<http://powo.science.kew.org>) and International Plant Names Index (<https://www.ipni.org>): *Pinus strobiformis*; *P. arizonica* (syn. *P. ponderosa* var. *arizonica*); *P. discolor* (syn. *P. cembroides* var. *bicolor*); *P. engelmannii*; *P. chihuahuana*; (syn. *P. leiophylla* var. *chihuahuana*).

Species name	<i>Pinus strobiformis</i>	<i>Pinus arizonica</i>	<i>Pinus discolor</i>	<i>Pinus engelmannii</i>	<i>Pinus chihuahuana</i>
	Southwestern white pine Pino huiyoco	Arizona pine Pino blanco	Border pinyon Piñón, pino piñonero	Apache pine Pino real	Chihuahua pine Pino chino, pino chimonque
Geographic focus					
Northern	Intermediate shade tolerance ⁴ Broad environmental tolerance ¹⁰ Associated with longer fire intervals ^{3, 14, 15}	Moisture availability and fire intervals related to stand dynamics ³ Thrives in disturbed sites with shade and exposed soil ¹⁴ Tree establishment is associated with longer fire intervals ^{3, 14, 15}	Water stress controls lower elevational limits; exhibits both drought resistance and tolerance of cold, more mesic conditions at higher elevations ⁴	Water stress controls lower elevational limits; post-fire increase in light and temperature favorable to seedlings ⁴ Sensitivity to water stress after wildfire can limit regeneration ^{12, 13}	Water stress controls lower elevational limits; low light and deep litter control upper elevational limits; less shade tolerant than higher elevational pines ⁴ Potential for adaptation to warmer temperatures, reduced soil productivity, and wildfires ⁹ Sensitivity to water stress after wildfire can limit regeneration ^{12, 13}
Southern	Linked to elevation and solar radiation, great temperature fluctuations across the year; large spatial distribution and niche breadth ¹ Tolerant of semi-arid conditions ⁶ Found in mesic sites in pine forests ⁸ Inhabits northern aspect slopes and topographically sheltered sites ¹⁰	Moderately sensitive to climate change ⁶ Responds to changes in drought severity & cumulative water deficit ⁷	Dry to moderately summer-warm open mountain slopes, mild climate, variable rainfall, elevation and maximum temperatures, open & mixed pine-oak ² Sensitive to drought severity ⁷ Found in semi-dry temperate areas in pine-oak forests ⁸	Highly to moderately sensitive to climate change ⁶ Sensitive to drought severity ⁷ Found in semi-dry temperate areas in pine-oak forests ⁸	
Region-	Large range	Inhabits	More drought		More drought

wide	shift and contraction forecast; occurs in areas with high winter precipitation and low warmest month temperature ¹¹	mesic, north-facing slopes or canyon bottoms ⁵	tolerant than other pines ⁵	tolerant than other pines ⁵
¹ Aguirre-Gutiérrez et al. 2015		⁷ González-Cásares et al. 2017		¹³ Poulos et al. 2020
² Ávila-Flores et al. 2016		⁸ González-Elizondo et al. 2013		¹⁴ Iniguez et al. 2008
³ Barton et al. 2001		⁹ Hess and Fule 2020		¹⁵ Iniguez et al. 2016
⁴ Barton 1993		¹⁰ Looney and Waring 2013		
⁵ Ferguson et al. 2013		¹¹ Shirk et al. 2018		
⁶ Gómez-Mendoza and Arriaga 2007		¹² Barton and Poulos 2018		

Field data and derivation of species' presence/absence variables

We combined observations of pines from field studies conducted in the sky islands of México (Flesch et al. 2016; Flesch 2019) and the United States (Ganey et al. 1996; Sanderlin et al. 2013) to generate presence and absence data for each species (Fig. 1, Table 1). In México, vegetation data were gathered within 50 m of 1104 sampling points placed non-randomly in representative areas in major montane vegetation communities from 2009-2012. The majority of sky islands that support pines were sampled (Ferguson et al. 2013).

In the United States, data were collected within 318 plots between 2014 and 2015 (Sanderlin et al. 2014). Trees (> 10 cm diameter at 1.4 m above ground) distinguished by tree species were recorded within 0.1 ha circular plots (17.8-m radius). Plots were located along transects typically consisting of 12 points spaced at 300 m intervals (Sanderlin et al. 2013; Ganey et al. 2017), with transects being proportional to the approximate coverage of each montane vegetation type in the landscape.

For the response variable in species distribution models, species were considered present when that species was recorded as a tree within the sampled plot and absent when it was not recorded at the plot. Total sample sizes after combining observations from the México and United States field studies were $n = 1422$ for all species except *P. discolor* ($n = 1204$); a subset of plots did not include data for this species. Frequencies of occurrence for each species across datasets were: *P. strobiformis* 14%; *P. arizonica* 35%; *P. discolor* 23%; *P. engelmannii* 30%; *P. chihuahuana* 17% (see Maps of presence and absence data, Online Resource 2).

Using field data provided distinct advantages over more commonly used data in species distribution modeling which are often comprised of gridded species' occurrence records with coarse spatial resolution (Araújo and Guisan 2006). Field data used in our analysis include reliable absence records that are especially important in estimating probabilities of occurrence by comparing environmental characteristics at sites where the species was observed with those at sites where it was not observed (Guisan and Thuiller 2005; Guillera-Aroita et al. 2015).

Disadvantages of the sampling designs of the field studies include spatial bias (Araújo & Guisan, 2006) towards larger mountain ranges and potential for missing variability in mountain ranges where pines were assumed to be absent. Therefore, in some locations, predicted probabilities may reflect potential rather than actual distribution. Lower predictive ability may also result from factors not considered in the study design (i.e., island size, area of vegetation type) but should not obscure relationships to topography that define microrefugia.

Assembly of predictor variables

We assembled spatial layers of predictor variables across the geographic extent of each sky island complex (as defined by Deyo et al. 2013). We sampled the spatial layers at the field plot locations using the extract function in the R raster package (method=bilinear; Hijmans 2019). The dataset of predictor variables was appended to each species presence and absence database for use in modeling species distributions.

Terrain metrics were calculated from a 30 m Shuttle Radar Topography Mission (SRTM; Farr et al. 2007) digital elevation model (DEM) using SAGA-GIS (Conrad et al. 2015). Metrics included local morphometrics, characteristics of the catchment basin, relative position, and terrain ruggedness (Table 2). The slope position metrics describe locations relative to surrounding landscape, for example, Valley Depth is defined as the difference between elevation and an interpolated ridge level. Slope position metrics represent hillslope scale variations in moisture availability and microclimate (Hoylman et al. 2019).

Table 2. Predictor variables using in species distributions models, data sources, software used and definitions. Models were developed using 1) terrain metrics only; 2) top four predictors from the terrain model plus two remote sensing indices (NDVI or NDMI); 3) top four predictors from the terrain model plus two bioclimatic variables (TD and AHM).

Variable name	Source, description
Terrain metrics	30 m DEM, SAGA-GIS
Aspect	Local downslope direction with maximum rate of change (radians)
Slope	Local maximum rate of change in elevation (radians)
Elevation	Height above sea level (m)
Catchment Area	Size of the contributing area (m ²)
Catchment Slope	Average slope of the contributing area (radians)
Mid-Slope Position	Intermediate slope position between high and low (0-1)
Slope Height	Vertical distance from the base of the slope to its crest (m)
Valley Depth	Vertical distance to a channel network base level (m)
Terrain Ruggedness Index (TRI)	Sum of the differences in elevation between a cell and its surrounding cells, calculated in 210 m radius (7 x 7 30-m cell) moving window
Remote Sensing Indices	Composites of 30 m Landsat imagery, Google Earth Engine
Normalized Difference Vegetation Index (NDVI)	Spring (2011-03-01 to 2011-05-30) and Monsoon (2010-08-01 to 2010-10-30)
Normalized Difference Moisture Index (NDMI)	Spring (2011-03-01 to 2011-05-30) and Monsoon (2010-08-01 to 2010-10-30)
Bioclimatic Variables	Normals period (1981-2010), AdaptWest
Temperature Difference (TD)	Difference between Mean Temperature of the Coldest Month (°C), and Mean Temperature of the Warmest Month (°C)
Annual Heat Moisture Index (AHM)	(Mean Annual Temperature + 10)/Mean Annual Precipitation/1000)

Using Google Earth Engine cloud computing platform (Gorelick et al. 2017), we developed two median pixel top-of-atmosphere (TOA) reflectance composites of cloud-free 30 m Landsat Thematic Mapper imagery representing two distinct seasons: the summer monsoon (composite period: August 1, 2010 – October 30, 2010) and the spring growing season (composite period: March 1, 2011- May 30, 2011) (Table 2; Fig. 2). For each seasonal composite, we calculated the Normalized Difference Vegetation Index (NDVI) as a proxy for canopy structure and chlorophyll content (Gamon et al. 1995) and Normalized Difference Moisture Index (NDMI) as a proxy for vegetation liquid water content (Gao 1996).

We included two bioclimatic variables, Temperature Difference (TD) and Annual Heat Moisture Index (AHM) calculated for the normals period 1981-2010 at 1 km spatial resolution (AdaptWest Project 2015; Wang et al. 2016) (Table 2). We selected AHM and TD based on their importance in a principal components analysis of climate in the region (Villarreal et al. 2020). Climate normals (1981-2010) for TD and AHM had low correlations (Pearson's $r < 0.50$) with each other as well as terrain and remote sensing predictors. The 1981-2010 normals period overlapped or just preceded dates of field data collection.

The AHM variable is derived from Mean Annual Temperature (positive correlation) and Mean Annual Precipitation (negative correlation) (Table 2); temperature and water balance impose limits on plant reproduction and regeneration (Barton et al. 2001; Crimmins et al. 2011; Hess and Fule 2020). Differences in winter and summer temperatures determine TD values; TD represents variability in coastal influences on temperature extremes (Table 2). In the context of the current warming trend, less warming is generally expected to occur in locations that are nearer to coastlines (i.e., low TD; Ashcroft et al. 2009).

Model development and spatial predictions

We developed species distribution models using boosted regression trees, a method which incorporates advantages of tree-based methods and improves performance by fitting many models and combining them for prediction (Elith et al. 2008). We developed the models using the R packages *gbm* (Greenwell et al. 2019) and *dismo* (Hijmans et al. 2017). All models were parameterized using the Bernoulli family (for presence and absence data); the proportion of observations used in selecting variables was set to 0.5; complexity of individual trees was 5. To parameterize the learning rate, we started with $\eta=0.01$ and adjusted to a slower rate ($\eta=0.005$ or 0.001) to improve performance. We used 10-fold cross validation for model tuning and evaluation. Accuracy was evaluated using mean area under the receiver operating characteristic (ROC) curve (AUC) for the cross validations, which is most useful when the goal is predicting realized distributions and when data include known absences (Jiménez-Valverde 2012).

We constructed a terrain-only model (nine variables) and three additional models using the top four terrain predictors: terrain-bioclimate (AHM and TD); terrain-NDMI (spring and monsoon); and terrain-NDVI (spring and monsoon). We graphed partial dependence functions (R package *pdp*; Greenwell 2017) for the three variables with highest relative influence in the terrain-bioclimate models and evaluated the trends in terms of local and broader-scale climate relationships.

We mapped pine species distributions (probability of occurrence) at 1 km resolution based on the terrain-bioclimate model and the terrain-NDVI model using the *predict* function in the R raster package (Hijmans 2019). Spatial predictions were smoothed using a Gaussian kernel in a 7 x 7 cell window (3-km radius) to improve visualization of clusters of similar values (e.g., hotspots) while maintaining a continuous scale of predicted probability. We compared the two distribution maps for each species to identify distinct geographic trends.

Results

Terrain variables provided important information in pine species distribution models and additional predictors resulted in further improvement. Average AUC values were generally high for all five species (Table 3). Specifically, model fit statistics show that the addition of bioclimate and remote sensing variables to terrain predictors improved the terrain-only models, especially for *P. engelmannii* and *P. discolor* (Table 3; see Online Resource 3 for ROC plots). Models for *P. strobiformis* had consistent values of AUC (≥ 0.80). The models for *P. arizonica* and *P. engelmannii* were lower overall, compared with models for other species (AUC mean < 0.80). Models that included terrain and bioclimate variables had the best fit for all species except *P. engelmannii* which showed greater improvement with the addition of spring and monsoon NDVI to the best four terrain variables.

Table 3. Cross validation statistics for sky island pine species distribution models. The AUC mean for the 10-fold cross validations from generalized boosted regression is given for each of the four models developed for the five pine species. Highest AUC values, indicating the best-fit model, are highlighted for each species.

Species	All terrain predictors	Top four terrain + AHM + TD	Top four terrain + two remote sensing variables	
	AUC mean	AUC mean	AUC mean NDMI	AUC mean NDVI
<i>P. strobiformis</i>	0.815	0.844	0.828	0.831
<i>P. arizonica</i>	0.747	0.765	0.764	0.763
<i>P. discolor</i>	0.765	0.888	0.803	0.807
<i>P. engelmannii</i>	0.649	0.710	0.709	0.713
<i>P. chihuahuana</i>	0.745	0.803	0.760	0.767

The top four terrain predictors of pine species distributions (i.e., those included in Table 4 results) included terrain ruggedness (TRI) for *P. strobiformis*, *P. engelmannii* and *P. chihuahuana* and aspect for *P. arizonica* and *P. discolor*. Characteristics of the catchment basin were important in *P. strobiformis*, *P. arizonica* and *P. discolor* models. At least one of the relative height metrics (slope height, mid-slope position and valley depth) appeared in all models but were never top predictors in the terrain-bioclimate models.

Table 4. Relative influence statistics as indicators of variable importance from generalized boosted regressions. Percent relative influence is given for the terrain-bioclimate models (A) and the terrain-NDVI boosted regression models (B). TRI = Terrain Ruggedness Index; TD = Temperature Difference; AHM = Annual Heat Moisture Index. Best-fit models (from Table 3) are starred.

A.

<i>Pinus strobiformis</i>		<i>Pinus arizonica</i>		<i>Pinus discolor</i>		<i>Pinus engelmannii</i>		<i>Pinus chihuahuana</i>	
Terrain-bioclimate model**		Terrain-bioclimate model**		Terrain-bioclimate model**		Terrain-bioclimate model		Terrain-bioclimate model**	
AHM	39.64	Elevation	54.29	TD	33.51	Elevation	31.52	Elevation	27.59
Elevation	29.02	AHM	12.12	AHM	19.81	TD	23.35	AHM	23.61
TRI	9.39	Aspect	9.83	Elevation	16.43	AHM	18.83	TD	19.85
Slope Height	9.27	Slope Height	8.73	Aspect	10.57	Mid-slope Position	10.16	Slope Height	10.84
TD	6.44	TD	8.20	Catchment Slope	10.39	TRI	8.60	Valley Depth	10.76
Catchment Slope	6.20	Catchment Area	6.80	Slope Height	9.25	Slope Height	7.51	TRI	7.31

B.

<i>Pinus strobiformis</i>		<i>Pinus arizonica</i>		<i>Pinus discolor</i>		<i>Pinus engelmannii</i>		<i>Pinus chihuahuana</i>	
Terrain-NDVI model		Terrain-NDVI model		Terrain-NDVI model		Terrain-NDVI model**		Terrain-NDVI model	
Elevation	52.26	Elevation	64.07	Elevation	27.39	NDVI monsoon	30.38	Elevation	43.15
NDVI spring	15.74	NDVI spring	12.66	NDVI spring	20.11	Elevation	28.87	Slope Height	17.87
Slope Height	9.58	NDVI monsoon	7.67	NDVI monsoon	16.14	NDVI spring	17.84	NDVI monsoon	11.46
TRI	8.09	Slope Height	5.59	Catchment Slope	14.25	TRI	8.97	NDVI spring	10.55
NDVI monsoon	7.58	Aspect	5.10	Slope Height	11.83	Mid-slope Position	8.47	Valley Depth	9.75
Catchment Slope	6.73	Catchment Area	4.88	Aspect	10.25	Slope Height	5.44	TRI	7.19

Elevation and one or both bioclimate variables comprised top predictors of pine species distributions in the terrain-bioclimate models, based on relative influence (Table 4-A). In the *P. arizonica* models, the predominance of elevation was especially notable (relative influence = 54%). Two climate variables exhibited high relative influence in *P. discolor*, *P. engelmannii*, and *P. chihuahuana* models (relative influence > 16%). In *P. strobiformis* and *P. arizonica* models, AHM and terrain metrics (i.e., TRI and aspect) had greater weight than TD.

Models that included NDVI variables showed different order of importance, e.g., NDVI monsoon was the top predictor for *P. engelmannii* distribution; all other species had elevation as the top predictor (Table 4-B). NDVI spring was the second most influential predictor in *P. strobiformis*, *P. arizonica*, and *P. discolor* models. Three species had both spring and monsoon NDVI as top three predictors: *P. arizonica*, *P. discolor*, and *P. engelmannii*. Terrain-NDMI results were not reported, due to similar AUC values compared with models that included seasonal NDVI.

Pine species exhibited specific affinities for elevation zones (Fig. 3; right column); *P. strobiformis* and *P. arizonica* were most common at highest elevations, reaching plateaus in predicted probability in areas greater than 2500 m. In contrast, *P. discolor* had the greatest positive response to elevation in a narrow, low elevation zone; a more variable change in response was observed at middle elevations. Species associated with lower elevations, i.e., *P. engelmannii* and *P. chihuahuana* differed in response pattern; *P. engelmannii* exhibited a more gradual decline as elevation increased and in contrast, *P. chihuahuana* response declined precipitously at approximately 2000 m.

Species common at higher elevations (*P. strobiformis* and *P. arizonica*) were associated with lower values of AHM (Fig. 3; left column). For *P. strobiformis*, predicted probability of occurrence increased with terrain ruggedness (TRI), and *P. arizonica* was more likely found on northern and northwesterly aspects (Fig. 3; middle column). In contrast, species common at mid- to lower elevation (*P. discolor*, *P. engelmannii* and *P. chihuahuana*) always included both bioclimatic variables in the top three set of predictors (Fig. 3; left and middle columns). Species presence was greatest in the middle to high range (*P. discolor* and *P. chihuahuana*) or lower range (*P. engelmannii*) of TD.

High probability of occurrence for the pine species had distinct geographic patterns with respect to latitude in both terrain-bioclimatic and terrain-NDVI models (Fig. 4 and Fig. 5). Hotspots (highest probabilities) for high elevation species (*P. strobiformis* and *P. arizonica*) were primarily limited to northern islands. In contrast, *P. discolor* high occurrence probabilities had a broad geographic range that stretched across the northern and central portions of the region. The only species limited to southern parts of the region was *P. engelmannii*. Maximum occurrence probabilities for *P. chihuahuana* were scattered across the islands, with clusters of higher values in central and southern latitudes.

General patterns in spatial predictions were similar, comparing the terrain-bioclimatic results (Fig. 4) with the terrain-NDVI results (Fig. 5) but the magnitude of predicted probability of occurrence differed. Differences between spatial predictions for *P. strobiformis* and *P. arizonica* distributions were minor, however, greater differences in probability were observed for other species. The terrain-bioclimatic models resulted in higher probabilities overall for *P. discolor* than the terrain-NDVI models with the exception of near zero probabilities in the far south. The *P. engelmannii* probability values were higher on some western islands, based on terrain-bioclimatic models; terrain-NDVI models predicted higher maximum probabilities in the southern-most islands. Terrain-bioclimatic models for *P. chihuahuana* exhibited higher probabilities across middle and lower latitudes within its elevational range, with one notable hotspot on Peloncillo-Pan Duro (Fig. 4). In contrast, terrain-NDVI models for *P. chihuahuana* included some areas with probabilities in the medium range in more northern islands (Fig. 5). Pine species associated with lower heat-moisture balance (*P. strobiformis* and *P. arizonica*; Fig. 4) also showed a strong relationship with Spring NDVI, conversely species that tolerated higher heat-moisture were associated with Monsoon NDVI (*P. engelmannii* and *P. chihuahuana*).

Discussion

Climate refugia for pines were evident within the highly variable environments found on isolated mountains of the Madrean sky islands where topography provides deterministic control on habitat and potentially reduces the rate of climate change in microrefugia (Fig. 3 and 6). We identified a wide variety of settings for the formation of microrefugia across the region, described by complex topography within preferred elevational zones (Fig. 6). The availability of presence and absence data from field studies and a fine scale digital elevation model enabled us to identify microrefugia as a primary focus. At a regional scale, we identified clusters of high predicted probability, or hotspots, that circumscribe climate refugia essential to pine conservation: a northern range for *P. strobiformis* and *P. arizonica*; north-central locations for *P. chihuahuana* and *P. discolor*, and across more southern islands for *P. engelmannii* (Fig. 4, 5 and 6).

Characteristics of pine microrefugia

Among the pines of the study region, resilience in forecasted warmer and drier climate may vary among co-occurring species (González-Cásares et al., 2017). The varied characteristics of microrefugia will provide important contributions to species resilience where topography slows local rates of climate change (Fig. 6). Each species preferred a specific range of elevation that corresponds to gradients in temperature, moisture and seasonality and regulate physiology and growth (Whittaker and Niering 1965; Barton 1993; Landsberg and Waring, 1997; Guisan and Thuiller 2005). The overlap in affinities across elevation reflects diversification of pine forests and woodlands where multiple species form communities (Fig. 3).

Across elevation, variability in terrain ruggedness, slope position and aspect were important factors in species distribution models (Fig. 3, Online Resource 4) that contribute to defining microrefugia. Specifically, local depressions associated with rugged terrain preferred by *P. strobiformis* (Fig. 3) are more sheltered from wind and desiccation (Dobrowski 2011). Microrefugia for *P. engelmannii* were associated with a low range of temperature difference (i.e., greater coastal influence), suggesting that in its optimal range of predicted probability, habitat for this species will be subject to slower rates of climate change than locations in the broader landscape.

Distinct thresholds defined microrefugia for some species, where small changes in elevation and bioclimatic variables resulted in a dramatic shift in species response. Thresholds occur where a physical limit is reached or shift in functional response occurs (Romme et al. 1998). For example, *P. chihuahuana* probability of occurrence declined precipitously between ~1800 and 2100 m elevation, and notably in a narrowly defined range of temperature difference (Fig. 3). In contrast, *P. arizonica* exhibited a continuous, but variable, increase in response across elevations above ~1800 m and a steady decline with increase in heat moisture (AHM; Fig. 3). In some cases, pine species were entirely absent from specific elevation zones, evidenced by plateaus in response at upper or lower extremes in elevation. For example, *P. strobiformis* was absent below ~2000 m and *P. engelmannii* was absent above ~2250 m (Fig. 3).

Species that occur in a narrow range of climate variability may experience an isolation effect that acts as a barrier to competition and negative influences such as pathogens (Ashcroft et al. 2012). In contrast, species that exhibit tolerance to a wider range of conditions may be able to take advantage of variability along a climate continuum, dependent on species interactions and other factors. Species-specific trait responses, such as tight control of transpiration via stomatal closure exhibited by *P. strobiformis*, will play a role in acclimation to drier and warmer climate (Buchholz et al. 2020).

Microrefugia and seasonal climate response

Remote sensing indices have distinct advantages in capturing habitat characteristics, including differences in canopy structure and greenness, and reflecting locally heterogeneous conditions and ecological context at high resolution (Cord et al. 2014; Villarreal and Petrakis 2014; Copenhaver-Parry et al. 2017). In particular, seasonal reflectance characteristics can indicate changes in habitat due to anthropogenic and natural disturbances like stand replacing wildfires, drought, insect outbreaks or logging. Such recent and historical landscape changes influence the current distribution of species (vs potential) but were not otherwise accounted for in our models of microrefugia. Understanding seasonal changes in relation to microrefugia is especially important given the interactions between climate and forest disturbance (Villarreal et al. 2019b; Villarreal et al. 2020).

Our results indicate that seasonal remote sensing data are especially important for characterizing microrefugia for *P. engelmannii* and *P. chihuahuana*, two species that are widely distributed across a low to mid-elevation range (Fig. 3 and Online Resource 5). Pine habitats in the low to mid-elevation range exhibit spectral characteristics associated with a more open canopy structure, more specifically, greening of herbaceous understory or co-dominant plants in response to monsoon precipitation. The remote sensing variables were more important for species in some southern islands where fires occur regularly (Villarreal et al. 2020) and where climate and disturbance conditions are favorable for seedling establishment and regeneration. For example, *P. engelmannii* exhibits fire-adapted traits such as thick bark, self-pruning of dead branches and "grass stage" seedlings which enhance fire tolerance (Rodríguez Trejo and Fulé 2003). Models for *P. engelmannii* showed the most improvement with the inclusion of monsoon greenness, and greater local spatial variability of hotspot predictions was apparent in the remote sensing model (Fig. 5).

Spatial hotspots for *P. chihuahuana* exhibited a distinct northward shift when seasonal greenness was considered (Fig. 5), compared with terrain-bioclimate model predictions (Fig. 4). The affinity of *P. chihuahuana* with more open conditions that have a stronger ecosystem response to monsoon moisture contrasts with higher elevation pines that have more closed canopies and more subtle differences in canopy reflectance response during spring greening. These contrasting traits provide information that aids in distinguishing conifers at higher elevations with similar climatic conditions but located in more northerly habitats (Buermann et al. 2008).

Threats to pine refugia

The ability of sky island refugia to support pine species will be tested as climate continues to change. Climate warming is expected to increase drought stress reducing both forest productivity and growth while increasing tree mortality in semi-arid areas of the southwestern United States (Williams et al. 2013). Similarly, climate models predict increasing aridity and more frequent drought spells reducing long-term water availability in northwestern México (Cook and Seager 2013). Changes in fire frequency and severity attendant with climate change may produce conditions in which refugia could lose their functionality (Morelli et al. 2020).

The functioning of climate refugia for pine species in the sky islands is subject to the influence of dominant processes that vary across species distributions (Hampe and Petit 2005; Slaton 2015). Dispersal mechanisms, including long-distance dispersal and ability to tolerate changes in precipitation will influence persistence and movement upward into higher elevation zones for species such as *P. chihuahuana* and *P. engelmannii* (Table 1; Table 4). Local adaptations and ability to withstand drought stress will be important to success of northern populations of *P. arizonica* (Barton et al. 2001; Hess and Fule 2020; Fig. 4 and 5). Seed dispersal by animals offers potential advantages for long-distance dispersal in *P. discolor* (Copeland et al. 2018). In addition, the association

of border pinyon with dry conditions (warmer slope aspects; Online Resource 4; Barton 1993) could infer resilience where drought is a dominant factor.

Regional studies predict shifts in species distributions with climate change across the sky islands. For example, comparisons of recent and historical data provide evidence that mature pine forest communities in the Madrean sky islands and Sierra Madre Occidental have been declining due to climate and land use change (Flesch 2019). Increased habitat loss and habitat patch isolation were forecast for montane species including *P. strobiformis* using comparisons of current and future climate change scenarios (Yanahan and Moore 2019). By 2080, a large range shift and contraction has been predicted for *P. strobiformis* across its distribution in the United States and México (Shirk et al. 2018). Increased frequency of high-severity fire has been noted in upper elevations of some northern sky islands (Villarreal et al. 2020), where pine species with limited distributions, e.g., *P. strobiformis*, favor mesic environments.

Conservation implications

Climate refugia of the past have been important to the formation of global biodiversity hotspots (Myers et al. 2000; Harrison and Noss 2017). In pine forests and woodlands, areas of relatively greater climate stability may provide holdouts and stepping-stones critical to species survival with future change (Keppel and Wardell-Johnson 2015). Refugia are one of the key determinants of species' persistence in the longer term (Keppel et al. 2012) and in shorter-term movements that are more complex than simply uphill and poleward (Pecl et al. 2017). The large degree of environmental heterogeneity we observed across pine habitats shows promise for facilitating range shift dynamics and buffering of habitats from the negative effects of climate change.

Conservation and management strategies that incorporate refugia could mitigate the dire outcomes for pines forecast by previous studies. The location and effectiveness of refugia will play an important role in both survival of individuals and populations and the ability to redistribute into more favorable habitats through time (Simons-Legaard et al. 2013; Andrews et al. 2018). Recent studies indicate microrefugia played a role in survival of pines (i.e., *P. leiophylla* var *chihuahuana* and *P. engelmannii*) following a recent, large fire in the Chiricahua Mountains (Barton and Poulos 2018). In the Santa Catalina mountains, heterogeneous topography infers local protection from fire (Iniguez et al. 2008) that allows cohorts of *P. arizonica* to establish within longer fire intervals (Iniguez et al. 2016).

Disturbance plays an important role in determining the ability of trees to disperse to favorable locations (Serra-Diaz et al. 2015), especially at the margins of species' distributions (Slaton 2015; Travers-Smith and Lantz, 2020). Fire will likely play a similar role where pines occur at their northern margins within the Madrean ecoregion as it affects soil and light conditions that are essential for growth and survival of seedlings (Barton 1993). Species traits that promote seed dispersal, including by wind and animals, will be key to determining redistribution for particular species. Species that are reliant on animal-dispersed seed (i.e., *P. strobiformis* and *P. discolor*), have the ability to resprout (i.e., *P. chihuahuana*), or are fire-tolerant as grass-stage seedlings (i.e., *P. engelmannii*) may have an advantage given increased fire observed during recent timeframes on northern sky islands (Villarreal et al. 2020).

Specific conservation measures will need to be developed to effectively conserve pine populations across the bi-national Madrean sky islands in light of existing priorities within places that vary in land ownership and tenure. Networks of potential refugia could become a useful focus for collaborative conservation efforts across ownership

and political boundaries, based on areas with high probability of species occurrence identified in our study. Fire management has been identified as a unifying management theme in the Madrean sky islands (Villarreal et al. 2019a; Villarreal et al. 2020). In a restoration context, fine-scale information on pine refugia reported here could help identify areas for restoration and also protect refugia from risk of severe fire effects and shortened fire intervals. Moreover, activities to assist reforestation and migration are increasing in response to changing disturbance regimes that accompany climate change (Carbajal-Navarro et al. 2019). Spatial models of pine refugia will provide key data for prioritizing the allocation of resources for these efforts and thus increase the likelihood of success.

Declarations

Funding was provided by the USGS Land Change Science Program.

Conflicts of interest/competing interests.

Not applicable.

Ethics approval.

Not applicable.

Consent to participate.

Not applicable.

Consent for publication.

Not applicable.

Availability of data and material (data transparency).

Data used in the analysis are available online (<https://github.com/HaireLab/madrean-pines>; DOI will be assigned via Zenodo upon publication of the manuscript). Spatial data layers of predicted probability and remote sensing indices will be published on ScienceBase and accessible through Data Basin (<https://databasin.org/galleries/b27fbb9c42b849fe9029827095449d07/>).

Code availability.

Computer (R) code is available online (<https://github.com/HaireLab/madrean-pines>).

Authors' contributions.

All authors contributed to the study conception and design. Field data collection was done by Aaron D. Flesch, Jose M. Iniguez and Jamie S. Sanderlin. Data preparation was accomplished Sandra L. Haire and Miguel L. Villarreal; analysis was done by Sandra L. Haire. The first draft of the manuscript was written by Sandra L. Haire and Miguel L. Villarreal and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Figures

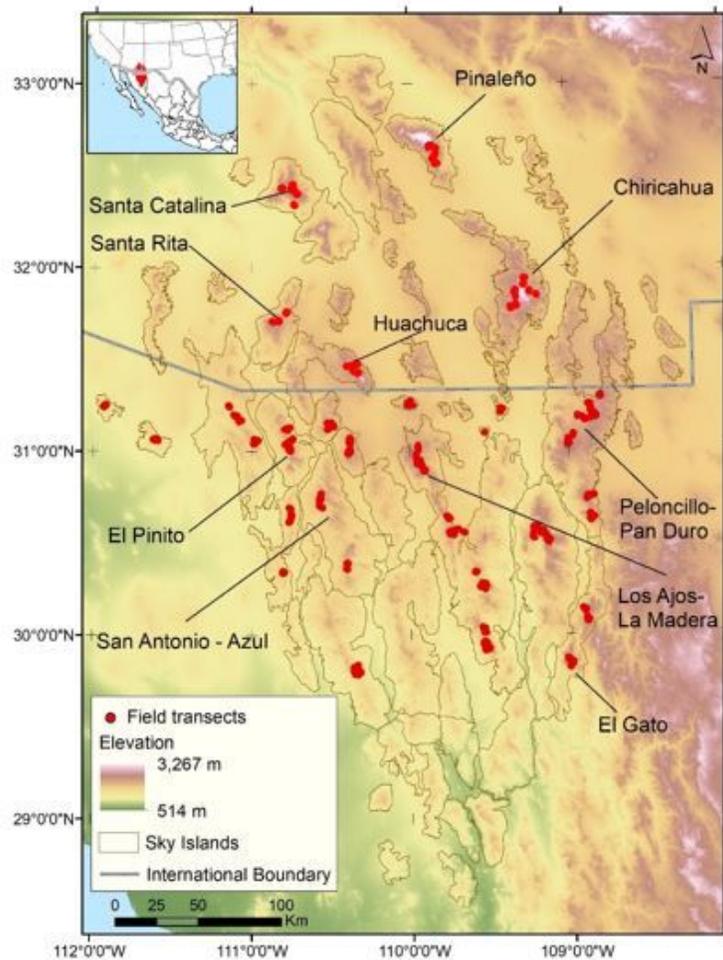


Figure 1

Elevation of the Madrean sky island study area with outline of island polygons (some island complexes are labeled for reference). Species distribution models were developed using field-based presence and absence data for pine species, recorded at sample locations (shown in red); terrain metrics, contemporary bioclimatic data; and remote sensing indices of greenness and moisture. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

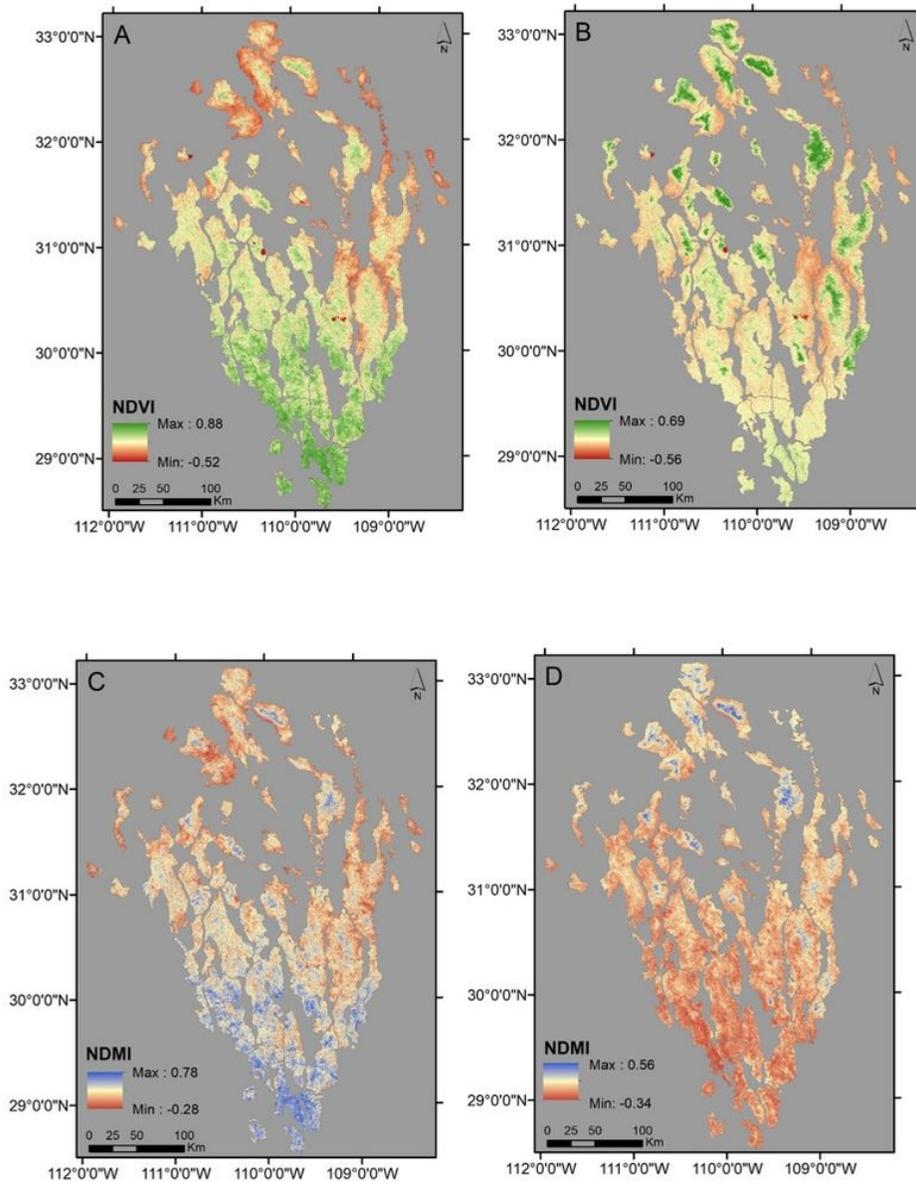


Figure 2

Monsoon (A) and Spring (B) Normalized Difference Vegetation Index (NDVI) and Monsoon (C) and Spring (D) Normalized Difference Moisture Index (NDMI) for the Madrean sky island study region. Minimum-maximum values are scaled to each composite image. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

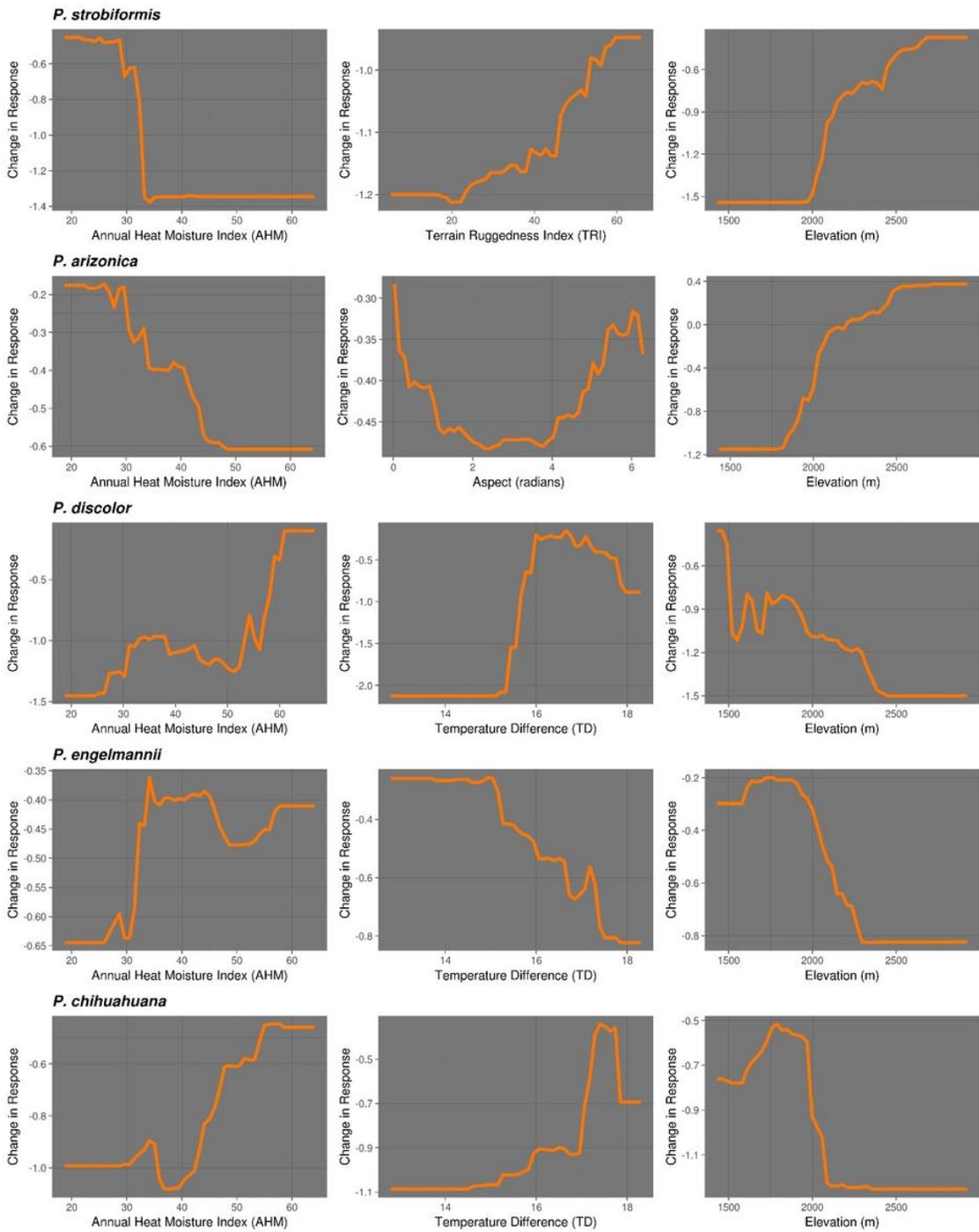


Figure 3

Partial dependence plots for the top three predictors from the terrain-bioclimatic model for each pine species included in the study (Table 4). Plots are arranged to aid comparisons across species in relation to Annual Heat Moisture Index (left column); either Temperature Difference or a top terrain predictor (center column); and elevation (right column). The y-axis scale represents the change in predicted probability relative to the predictor variable. Partial dependence plots for the top four terrain variables and partial dependence plots for the top three terrain-NDVI variables are located in Online Resource 4 and 5, respectively.

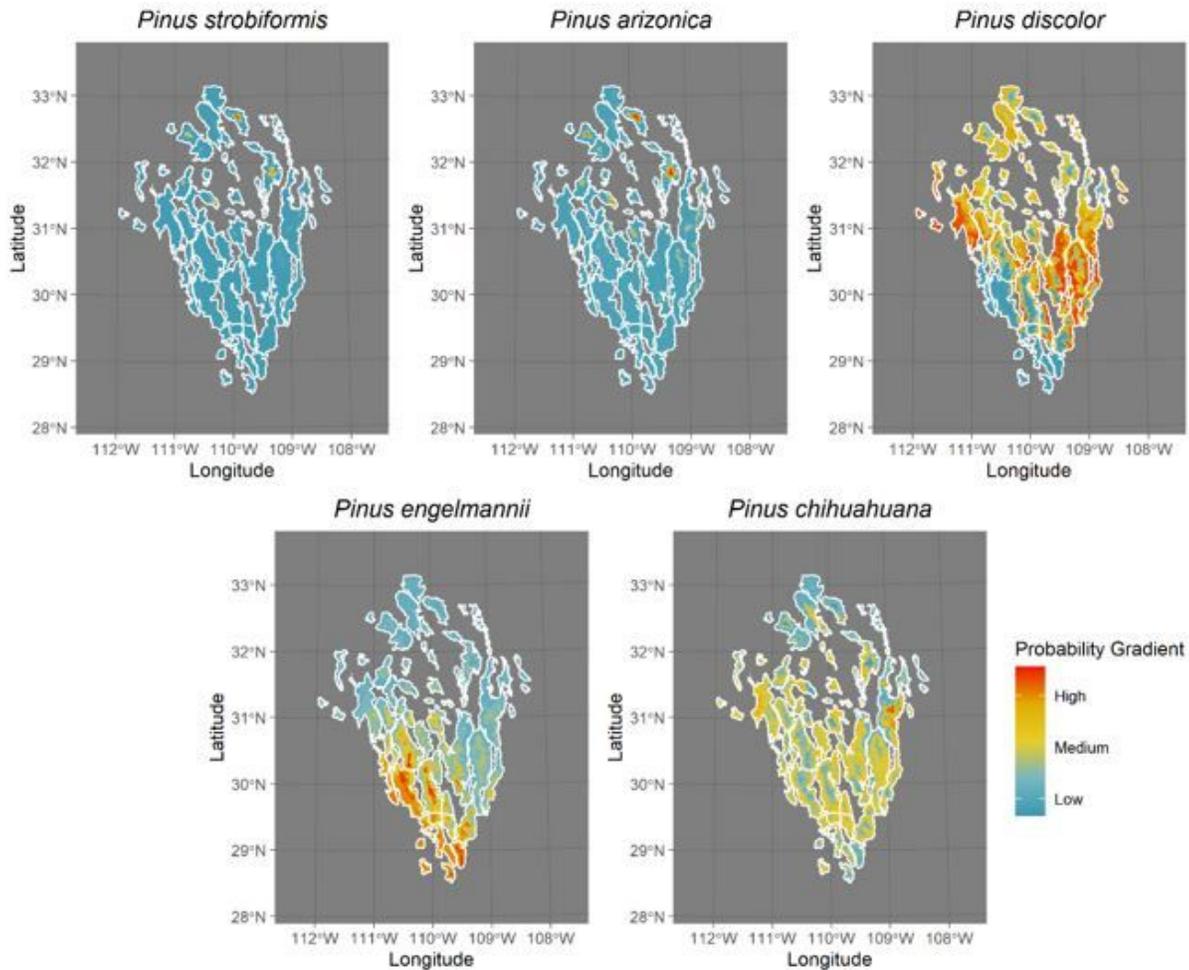


Figure 4

Spatial predictions of pine species distributions based on the terrain-bioclimatic model for each pine species included in the study. The predicted probabilities were smoothed to emphasize neighborhoods that differed in low, medium, and high probability. Areas of high probability, or hotspots, for *P. strobiformis* and *P. arizonica*, were clustered in northern islands. Hotspots for *P. discolor* were evident on western islands and continued across towards southeast and central locations. The only species with a distinctly south-southwestern distribution of high probability was *P. engelmannii*. Only one hotspot was evident for *P. chihuahuana*, located near the United States-México border on Peloncillo-Pan Duro (see Fig. 1).

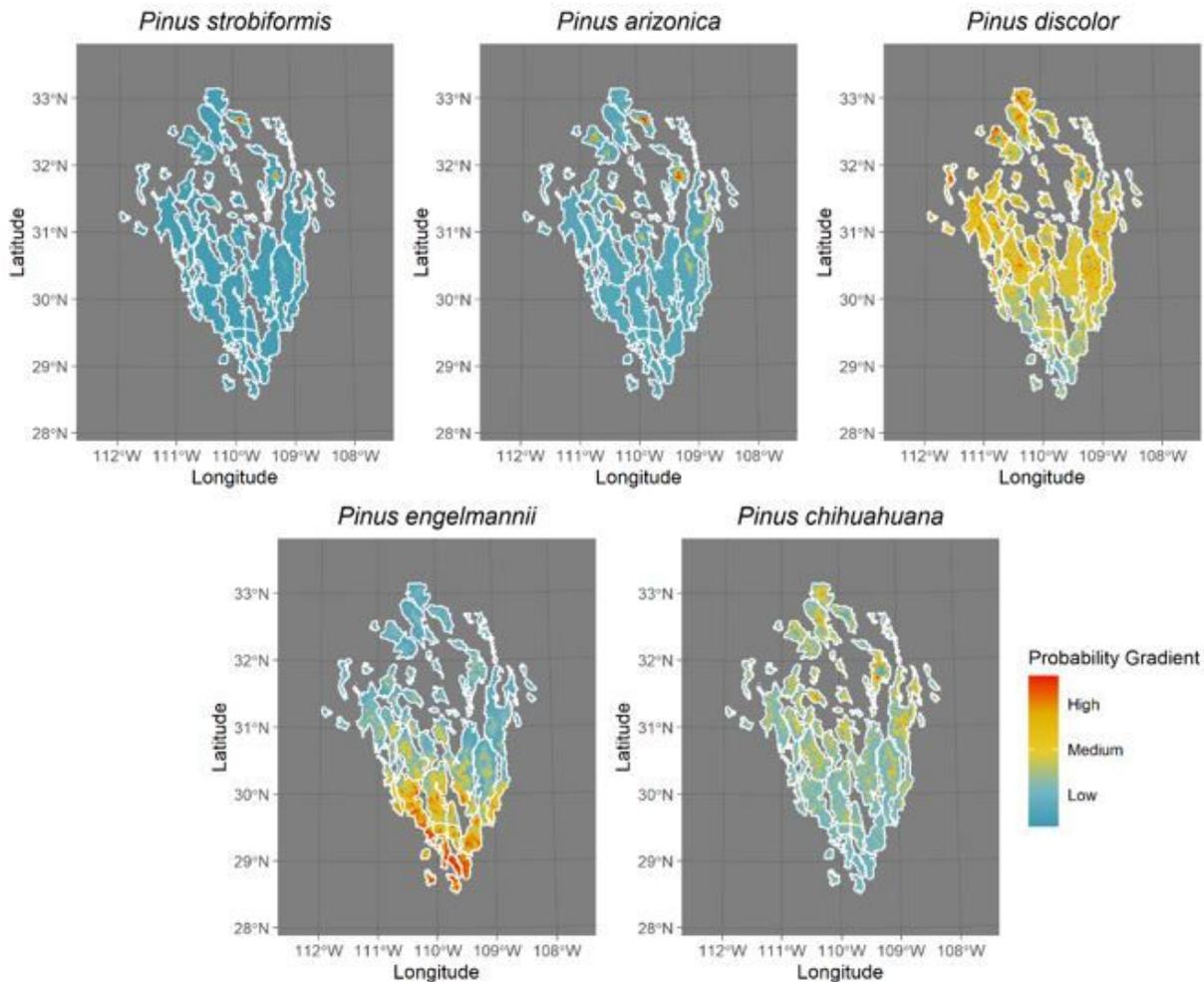


Figure 5

Spatial predictions of pine species distributions based on the terrain-NDVI model for each pine species included in the study. The predicted probabilities were smoothed to emphasize neighborhoods that differed in low, medium, and high probability. Similar to predictions from terrain-bioclimatic models (Fig. 4), areas of high probability, or hotspots, for *P. strobiformis* and *P. arizonica*, were clustered in northern islands. Hotspots for *P. discolor* were more prominent on western and northern islands and scattered across central islands. Areas of high probability for *P. engelmannii* were found at lower latitudes. Distinct hotspots for *P. chihuahuana* were absent, but compared to terrain-bioclimatic models, its distribution had shifted northward (see Fig. 4). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

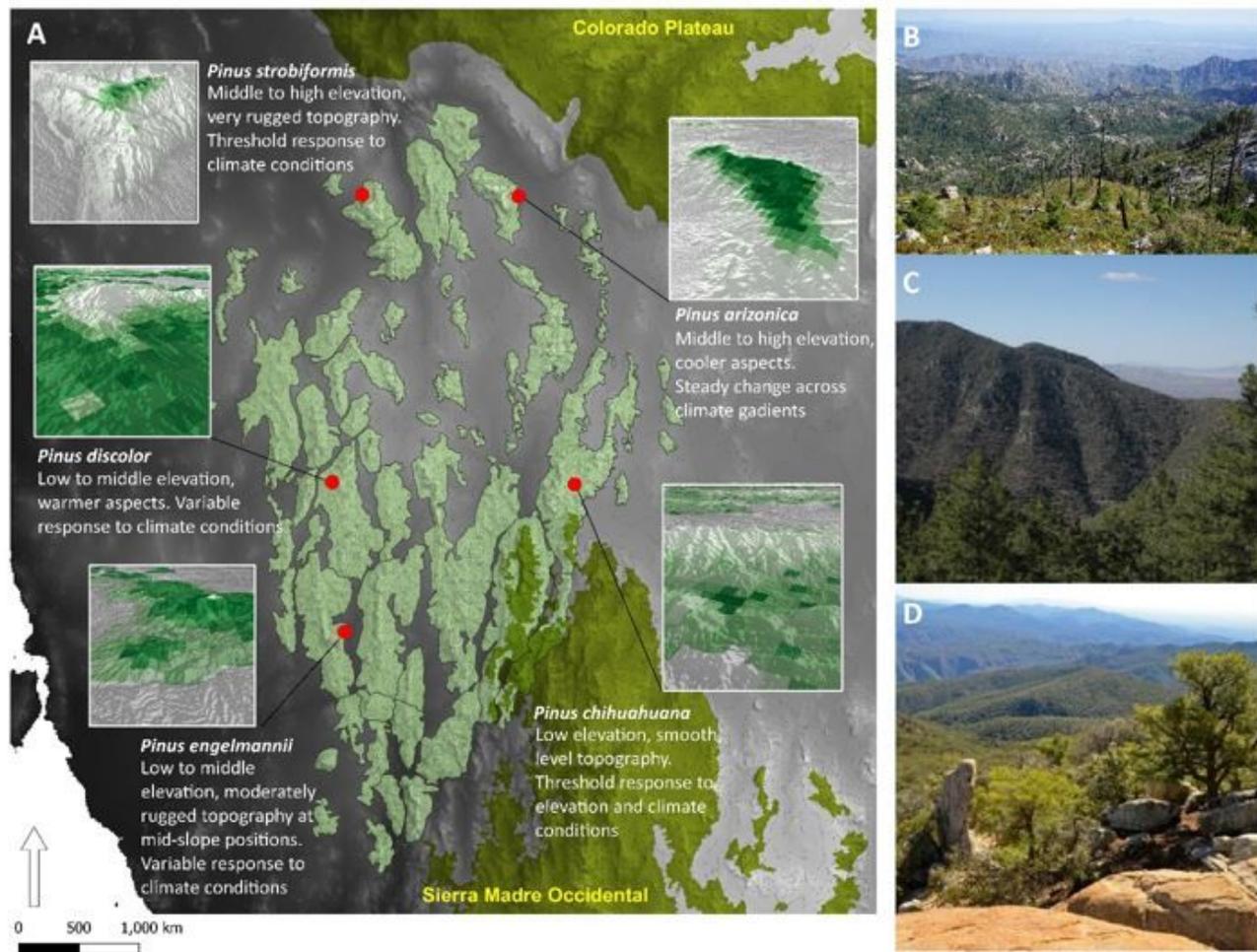


Figure 6

The Madrean sky islands form an archipelago of isolated mountain ranges between the Sierra Madre Occidental to the south and the Colorado Plateau to the north (map A). The sky islands are characterized by steep and rugged topography (photographs B,C and D). We identified a wide variety of settings for the formation of microrefugia across the region, described by complex topography within preferred elevational zones (map A insets: zoomed in predicted probability surfaces and text boxes). Map insets of spatial predictions illustrate hotspots of high probability in dark green, and corresponding text boxes describe preferred topographic and climate conditions for each species: we observed a northerly distribution of high probabilities for *P. strobiformis* (map A top left) and *P. arizonica* (map A top right) north-central distribution of *P. chihuahuana* (map A bottom right) and *P. discolor* (map A middle left) and more southerly distribution of *P. engelmannii* (map A bottom left). Photo locations: Santa Catalina Mountains (B); Sierra Aconchi (C); Sierra el Pinito (D). Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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