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Biogeography and Diversity of Pines in the Madrean Archipelago

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Abstract—*Pines are important dominants in pine-oak, pine and mixed-conifer forests across the Colorado Plateau, southern Rocky Mountains, Sierra Madre Occidental, and in the intervening Sky Islands of the United States-Mexico borderlands. All 17 native species of pines in the Sky Islands region or their adjacent mountain mainlands reach the northern or southern margins of their geographic ranges and most (12) have Madrean vs. Petran affinities. We compiled data on the occurrence and diversity of pines across 31 Sky Islands based on extensive fieldwork that complemented data from museum collections. Lower and smaller mountains supported zero to four species of pines whereas higher ones with greater area and thus larger population sizes supported five to seven species. Diversity of pines increased by 0.34% with each 1% increase in area (km^2) of forest in a mountain range with similar effects for maximum elevation ($P < 0.001$); diversity decreased by 0.70% with each 1% increase in distance (km) to the nearest mainland ($P < 0.015$). Forest area explained >2 times more variation in pine diversity ($R^2 = 0.42$) than distance from the nearest mainland ($R^2 = 0.19$), suggesting that larger population sizes of pines on bigger mountains reduce rates of stochastic extinctions and that this process is more important than dispersal limitation in driving pine diversity. Although pine species have no legal conservation status in the Sky Islands, pine forests, especially those on small isolated mountaintops, are among the most threatened plant communities in this region due to increased fire disturbance, insect outbreaks, and climate change.*

Introduction

The genus *Pinus* includes about 110 species and is the largest genus of conifers and among the most widespread trees in the northern hemisphere. Mexico and Central America support the highest diversity of pine species (47) including 30 that are endemic to Mexico, whereas a second center of diversity of about 25 species occurs in eastern Asia (Price and others 1998). As noted in 1942 by Howard Gentry, Mexico is a cornucopia of pine species with high diversity that crosses the United States-Mexico border into the Madrean Sky Islands region (Martin and others 1998). Of 17 native species of pines in the Sky Islands and their adjacent cordilleran mainlands, 12 have stronger biogeographic affinities to the more southerly Sierra Madre Occidental (SMO). Notably, in this broad biogeographic transition zone, all 17 species of pines reach the northern or southern margins of their geographic ranges.

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We studied the distribution of pines in the Madrean Sky Islands region and assessed how mountain area, elevation, and distance to the nearest mainland (SMO or Colorado Plateau) affected diversity of pines across 31 Sky Island mountain ranges in the United States and Mexico. We present these results and discuss implications for understanding the distribution, biogeography, and conservation of pines in the region.

Methods

Study Area

We considered three geographic areas: 1) mountain ranges across the entire Sky Islands region in southern Arizona, southwest New Mexico, northeast Sonora, and northwest Chihuahua, 2) the southern Colorado Plateau and Rocky Mountains (CP-RM) in southern Colorado, central and northern Arizona and northern and western New Mexico, and 3) the continuous highlands of the northern SMO in east-central Sonora and west-central Chihuahua that are located directly south and east of the Sky Islands region.

The Sky Islands region encompasses the Apachian subprovince of the Madrean floristic province (McLaughlin 1995, 2007, 2008) and is bounded to the north by the Gila River or by a level grassland plain in lowest saddle on the Continental Divide (1370 m). Although the region's southern boundary has been defined based on the biogeographic

affinities of the local flora, it is less clear exactly where it should be placed. The east and west boundaries of the Sky Islands region are more well defined by vast level plains of low relief beyond the Big Hatchet mountains in New Mexico and the Baboquivari mountains in Arizona/Sierra el Humo in Sonora, respectively (Marshall 1957; Flesch and Hahn 2005).

Design

We considered mountain ranges that supported at least one species of pine in the flora and that supported woodlands of oaks and pines that were isolated and discrete from other such patches. Mountain ranges containing pines have peak elevations greater than 1885 m, and we considered mountain ranges as discrete (a) if they were not connected by elevations >1555 m (the highest saddle with a wide grassland ecotone); (b) if there were no continuous woodland across a saddle if higher than 1555 m; and (c) if continuous woodland exists without pines if lower. The role of vegetation was important in determining three: (1) a desert grassland saddle at 1675 m between the Animas and Pan Duro/Sierra San Luis mountains separates them as islands on the eastern edge of the Sky Island region bordered by drier desert grassland and Chihuahuan desertscrub; (2) a continuous oak woodland saddle at 1350 m between the Sierra de los Ajos/Púrica and the Sierra Juriquipa that has a broad area connecting the ranges (on a rapidly rising Pacific slope gradient); and (3) a problematic zone noted by McLaughlin (1995) that includes highland extensions of SMO woodlands in the Sierra Hachita Hueca and El Gato (Huachinera) with saddles >1555 whereas the 2400 m high Sierra Bacadéhuachi is an island because of the low 1340 m saddle of oak woodland that separates Sierra Bacadéhuachi from more extensive woodlands of the SMO.

Data Collection and Analysis

We compiled information on the presence and distribution of pines during many years (1995-2011) of fieldwork. We supplemented these data with historical records from museum records and databases such as the Southwest Environmental Information Network (SEINet) and Madrean Archipelago Biodiversity Assessment (MABA) floral database (http://www.madrean.org) dating back to 1880. Information on pine distribution outside the Sky Islands region for determining extent and geographic center of species ranges was obtained from Little (1999).

Because the taxonomy of some species in the genus *Pinus* is equivocal, we verified species by examining representative specimens and used nomenclature from published sources (Farjon and Styles 1997; Ferguson and others 2001; García-Arevalo and González-Elizondo 1998; Kral 1993; Price and others 1998). Recent phylogenetic analyses based on molecular data and phytochemistry have provided new information on some of these taxonomic problems. Definitions of some of the more problematic species are defined in the Appendix.

To assess the effects of large-scale landscape and biogeographic factors on diversity of pines in the Sky Islands region, we used four variables. As a response variable we calculated the number of *Pinus* species found in the flora of each mountain island. As explanatory variables we considered total area of woodland and forest (km^2) that could potentially support pines, the maximum elevation of each mountain range from sea level to summit (m), and the distance from each mountain range to the nearest mainland or potential source population of immigrants (km; CP-RM or SMO). We only considered mountains that supported pines because we were interested only in these relict and isolated populations of the Holocene, rather than the broader dispersal routes of past climates.

To estimate the area of woodland and forest vegetation in each Sky Island, we used data from The Nature Conservancy's Apache Highlands Ecoregion study for mountains in Arizona, New Mexico, and northern Sonora and Chihuahua (Marshall and others 2004). For other mountain ranges in Mexico we used data from the Mexican National Forest Inventory and combined comparable vegetation communities (Palacio-Prieto and others 2000; Velazquez and others 2000). Using this first data source, we calculated woodland area for each mountain range by summing the areas among seven vegetation communities: Madrean Encinal, Madrean Oak-Pine Woodland, Pinyon-Juniper Woodland, Interior Chaparral, Montane Mixed-Conifer Forest, Ponderosa Pine Forest and Woodland, and Sub-alpine Spruce-Fir Forest and Woodland. For this second data source, we computed comparable estimates by summing the area of Chaparral, Bosque de Encino, Tascate, Encino-Pino, and Pino-Encino.

We used estimates of the maximum elevation of each Sky Island from USGS and INEGI topographic maps rounded to nearest 5 m. Distance estimates between each Sky Island and the CP-RM and SMO were obtained from 1:500,000 scale NOAA Sectional Aeronautical Charts and from Google Earth. We measured distances between the summit of each mountain range and a fixed reference point for each mainland. The CP-RM reference point was located at the southern edge of this highland at 2740 m elevation (33°33'N,109°20'W; near U.S. Highway 191 south of Hannagan Meadow, Arizona) and the SMO reference point was at the north edge of this highland at 2690 m elevation (30°33' N.,108°37'W.; Mesa las Guacamayas, Chihuahua).

To model the effects of area, elevation, and isolation on pine species diversity, we log transformed each variable and used simple linear regression to estimate the slope of each individual effect and the total variation in pine diversity that was explained by each explanatory variable. To assess the combined effects of different explanatory variables on pine diversity, we used multiple linear regression. Because maximum elevation was correlated with area of woodland and forest ($r = 0.41$, $P = 0.024$), we only used area and distance in the model. Because estimates from two mountain ranges were outliers, we conducted some analyses with and without these values. We also assess the effects of distance from the CP-RM or SMO on diversity of northern and southern pine species, respectively.

Results

Pine Species Occurrence and Diversity

A total of 17 pine species occur in the study area (table 1). Nine species of pines occur in 31 Sky Islands including five species that are widely distributed in the Sky Islands. The northern mainland (CP-RM) supports two species of pines (*Pinus aristata* and *P. contorta*) that do not occur at the southern edge of the Colorado Plateau or in the nearby Sky Islands. The southern mainland (SMO) supports five species (*P. herrerae, P. leiophylla, P. lumholtzii, P. maximinoi, and P. oocarpa*) in the north-central portion of the range that do not occur at the northern edge of the SMO or in the Sky Islands; a sixth Madrean species of pine (*P. cembroides*) does occur at the northern edge of the SMO but not in the Sky Islands.

The highest diversity of pines in a single Sky Island is seven species, occurring in the Chiricahua Mountains, the second highest elevation island. Of the other high islands, three have six species (Pinaleño, Huachuca, and Santa Rita) and the lower wider Galiuro Mountain also have six. The most diverse Sky Islands have about the same number of species as found at the edge of the CP-RM mainland (seven), in

Table 1—Biogeographic affinities and presence (X) of nine *Pinus* species in 31 Sky Islands and adjacent mainlands, with peak elevations for each island, from north (left) to south (right) in (A) southwestern U.S. and (B) northwestern Mexico.

		A																	B															
Floristic Subprovince	*Pinus* Species	(Colorado Plateau)	Santa Teresa	Pinaleño	Galiuro-Winchest.	Santa Catalina	Rincon	Little Dragoon	Dragoon	Chiricahua	Whetstone	Sierrita	Baboquivari	Santa Rita	Huachuca	Atascosa	Mule	Big Hatchet	Animas	Pan Duro-Pelon.	San José	Chivato	Pinito	Cibuta	Mariquita	Ajos	Azul	Madera Imuris	San Antonio	Tigre	Madera Oposura	Aconchi	Bacadéhuachi	(Sierra Madre)
Colorado Plateau and Rocky Mountains [a]	*P. flexilis*	X			X																													
	P. edulis	X	X	X	X					X								X																
	P. ponderosa	X	X	X	X	X	X			X	X			X	X						X													X
Madrean [b]	*P. strobiformis*	X		X		X	X			X				X	X				X	X	X				X	X	X			X	X		X	X
	P. chihuahuana		X	X	X	X	X			X				X	X	X			X	X	X		X	X	X	X	X	X	X	X	X	X	X	X
	P. arizonica			X	X	X	X			X				X	X				X	X	X		X		X	X	X			X	X	X	X	X
	P. discolor		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X		X	X	X	X			X	X		X	X	X				X
	P. engelmannii									X				X	X		X		X	X		X	X	X	X	X	X	X	X	X	X	X	X	X
	P. yecorensis																																X	X
TOTAL species per island:		4	6	6	5	5	0	1	7	2	1	1	6	6	2	2	1	5	5	5	2	3	2	5	5	4	3	3	5	4	3	5		
Elevation (m)		2525	3270	2340	2790	2640	2050	2290	2975	2350	1885	2360	2880	2885	1965	2245	2540	2600	2520	2520	2160	2200	2000	2480	2615	2440	2000	2220	2440	2320	2180	2400		

[a] Two additional species do not reach the Sky Islands: *P. aristata, P. contorta*.

[b] Six additional species do not reach the Sky Islands: *P. cembroides, P. herrerae, P. leiophylla, Pl lumholtzii, P. maximinoi. P. oocarpa.*

the CP-RM proper (six), or at the edge of the SMO (eight) although the species present in the north and south are different. With 13 pine species, the SMO has a much higher diversity than any individual Sky Island, although at any one location in the northern SMO only as many as 7 species co-occur.

Three biotic provinces (Madrean, Cordilleran, Apachian) of Dice (1943) are represented by the floristic elements defined by McLaughlin (2008). Of the 17 species of pines in our study area, five (~30%) have affinities to the northern floristic element of the CP-RM subprovinces and 12 (~70%) have affinities to a southern floristic element of the Madrean floristic province. Three Madrean element pines (*Pinus chihuahuana*, *P. discolor*, and *P. arizonica*) extend as far north as the edge of the CP-RM, and a fourth (*P. strobiformis*) extends onto the Colorado Plateau. One CP-RM element pine (P. ponderosa) extends to the edge of the SMO and onto the SMO proper in the northern part only.

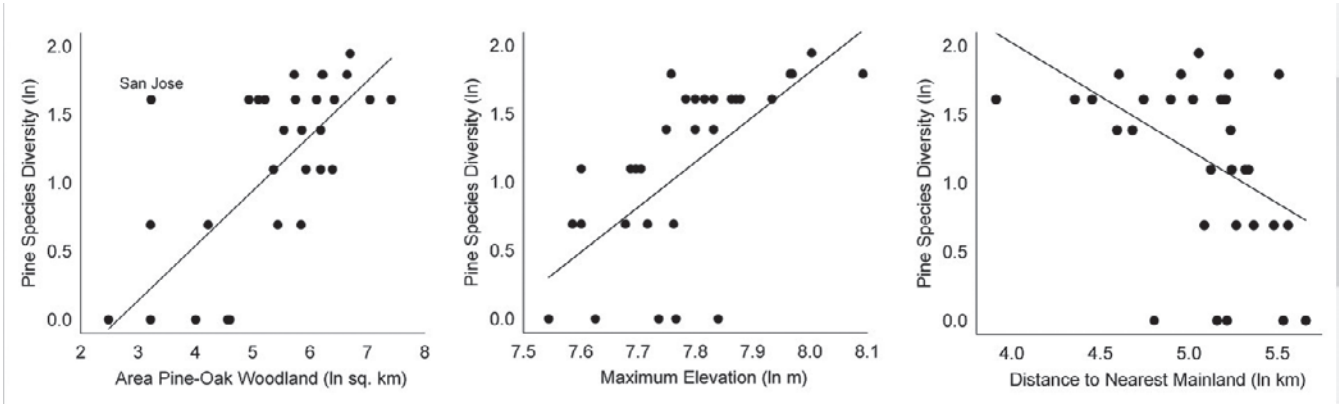

Figure 1—Relationship of pine species diversity (ln) to woodland area, elevation, and distance to the nearest mainland (left to right) in all 31 Sky Island mountain ranges in the Madrean Archipelago. The regression line is the estimate of diversity for each effect. An outlier for the effect of area is Sierra San José.

Drivers of Diversity

Both the area of woodland habitat and the maximum elevation of a Sky Island have large effects on diversity. Pine species diversity increased by 0.34 ± 0.074% (± SE) with each 1% increase in area of woodland (km2) that was present in a Sky Island ($P < 0.0001$; fig. 1) and by 3.20 ± 0.074% (± SE) with each 1% increase in elevation ($P < 0.0001$; fig. 1). The effect of area was large even with a Sky Island outlier, Sierra San José included. Island isolation also affected pine species diversity but explained less variation than area or elevation when considered independently (table 2). Species diversity decreased by 0.70 ± 0.27% (± SE) with each 1% increase in distance to nearest mainland ($P = 0.015$; fig. 1). We found that one Sky Island was an outlier with respect to the distance effect; when Big Hatchet was removed the effects of distance on pine diversity increased (table 2). Distance to the nearest mainland was not as correlated with either woodland area or elevation ($r = -0.37$, $P < 0.05$ and $r = -0.35$, $P = 0.05$ respectively).

When only pines species in the northern element were considered for each island, distance to CP-RM had a large effect on species diversity (table 3); species diversity decreased by 0.93 ± 0.15% (± SE) with each 1% increase in distance from the CP-RM ($P < 0.0001$; fig. 2). When only pines in the southern element were considered for each island, distance to the Sierra Madre had much less of an effect on pine species diversity; species diversity decreased by 0.36 ± 0.18% (± SE) with each 1% increase in distance from the SMO ($P = 0.065$; fig. 2) and by 0.47 ± 0.15% (± SE) with each 1% increase in distance once Big Hatchet was removed ($P = 0.004$; table 3).

When the combined effects of habitat area and isolation were considered, there was some evidence that both woodland area and isolation explained pine diversity (table 4). Species diversity increased by 0.30 ± 0.08% (± SE) with each 1% increase in the log number of km2 of woodland ($P < 0.0006$) after adjusting for the effect of distance to the nearest mainland, whereas, species diversity decreased by 0.38 ± 0.24% (± SE) with each 1% increase in log distance to the nearest mainland ($P = 0.12$) after adjusting for the area effect. With the Sierra San José and Big Hatchet outliers removed, the amount of variation in pine diversity that was explained by area and isolation increased somewhat ($R2 = 0.61$ vs. 0.47) and the effect of isolation became stronger.

Discussion

Biologists have tried to define factors that explain species diversity across the mountain islands of the western United States and assess how habitat area and isolation affect the distribution of population and diversity of communities. Some studies suggest that both factors are important in explaining diversity of montane birds and mammals in the borderlands mountains while other studies indicate habitat is more important than isolation (Gehlbach, 1995).

We found that these two variables, woodland area and distance to the nearest mainland, considered independently, were each good predictors of pine diversity across the mountain islands of the Madrean Archipelago. Maximum elevation was also considered a potential explanatory variable and found to be a significant predictor of pine species diversity (table 2). The relationship between a mountain's peak elevation and its area of woodland that supports pines can be attributed to the "Merriam Effect" (i.e. increase in orographic precipitation and adiabatic cooling with increases in elevation), so the larger the mountain island, the more conifer forest it contains (Gehlbach, 1981). In our study, maximum elevation and woodland area were correlated and essentially measured the same attribute—habitat area and thus population size of pines. Isolation distance explained less variation in pine species diversity than area, but did have some explanatory power even when adjusting for the effect of area (table 4.)

Table 2—Simple Linear Regression model for the effects of habitat area, elevation and distance to the nearest mainland on the diversity of pine species (ln) in all 31 Sky Island mountain ranges in the Madrean Archipelago and with one outlier removed.

Data set	Explanatory variable	R^2	Estimate	SE	*P*
All data					
	Area of pine-oak woodland (ln km^2)	0.42	0.34	0.07	<0.0001
	Maximum elevation (ln m)	0.43	3.20	0.69	<0.0001
	Distance to nearest mainland (ln km)	0.19	-0.70	0.27	0.015
Hatchet removed					
	Distance to nearest mainland (ln km)	0.26	-0.78	0.25	0.004

Table 3—Simple Linear Regression models for the effects of distance to the Colorado Plateau on the diversity of northern pine species (ln) and distance to the Sierra Madre Occidental on the diversity of southern pine species (ln) in all 31 Sky Island mountain ranges in the Madrean Archipelago and with one outlier removed.

Data set	Explanatory variable	R^2	Estimate	SE	*P*
All data					
	Distance to Colorado Plateau (ln km)	0.55	-0.93	0.15	<0.0001
	Distance to Sierra Madre (ln km)	0.11	-0.36	0.18	0.065
Hatchet removed					
	Distance to Sierra Madre (ln km)	0.26	-0.47	0.15	0.004

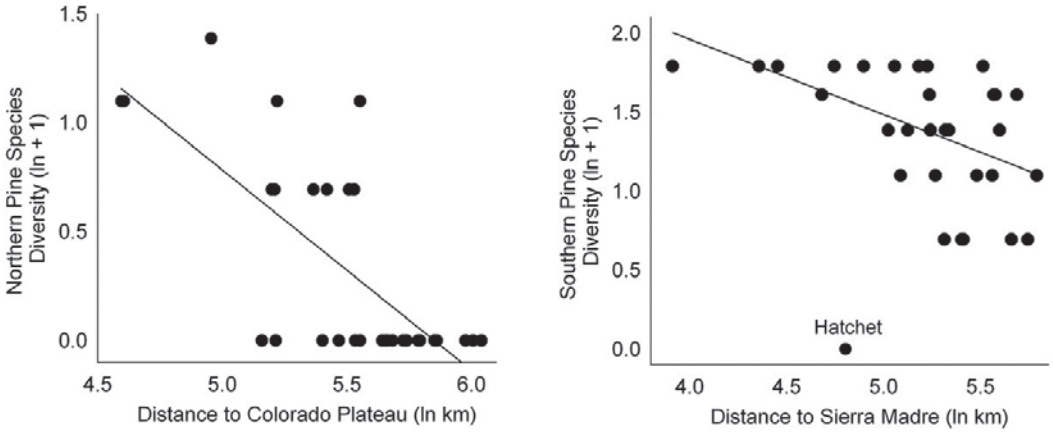

Figure 2—Relationship of pine species diversity (ln) to distance to the Colorado Plateau for northern pine species (left), and distance to the Sierra Madre Occidental for southern pine species (right) in all 31 Sky Island mountain ranges in the Madrean Archipelago. The regression line is the estimate of diversity for each effect. An outlier for the effect of distance on the diversity of southern pines is the Big Hatchet Mountains.

Table 4—Multiple Linear Regression model for the effects of habitat area and distance to the nearest mainland on the diversity of pine species (ln) in all 31 Sky Island mountain ranges in the Madrean Archipelago and with two outliers removed.

Data set	Explanatory variable	Estimate	SE	*P*
All data (R^2 = 0.47)				
	Area of pine-oak woodland (ln km^2)	0.30	0.08	0.0006
	Distance to nearest mainland (ln km)	-0.38	0.24	0.12
Hatchet and San Jose removed (R^2 = 0.61)				
	Area of pine-oak woodland (ln km^2)	0.33	0.07	<0.0001
	Distance to nearest mainland (ln km)	-0.38	0.20	0.074

In examining the distribution of reptiles and amphibian species, Swann and others (2005) found that none of the Sky Islands contain a full complement of southern species and that few reptile and amphibian species in the Sky Islands have affinities to areas north of the Sky Islands. For pines, none of the 31 Sky Islands contain a full complement of six southern element species although eight islands have five of the six species, and half of those are in Mexico. All Sky Islands with pines have at least one pine species of southern element in its flora with the exception of the Big Hatchet Mountains. Only one Sky Island has a full compliment of three northern element pine species. Of the 11 Sky Islands that have at least one northern pine species, just one mountain, the Sierra San José, is in Mexico.

An outlier in terms of the effect of distance from the southern mainland on the diversity of pines is the 2540 m high Big Hatchet Mountains. They are positioned close to the southern mainland and support no southern pines species. This could be associated with their longitude as they are at the easternmost edge of the of the Madrean Sky Islands and thus surrounded by the more arid adapted Chihuahuan desertscrub that is east of the Continental Divide, and the only high Sky Island composed entirely of limestone. The Florida Mountains and Cooke's Range farther east are not limestone, but also have the same single northern element pine species in their flora, *Pinus edulis*. A dispersal corridor may be to the north along the Continental Divide rather than to the SMO, despite a stepping stone in the adjacent Animas Mountains, which supports five southern pines. On floristic grounds, Big Hatchet is outside of the Apachian floristic subprovince (McLaughlin 1995, 2008).

An outlier in terms of the effect of woodland area on pine species diversity is the 2520 m Sierra San José, which has much higher diversity than expected given its small area. This pattern may be partly explained by latitude. Sierra San José is the second highest in elevation and the farthest north of any Sky Island in Mexico, but its mountain mass (ca. 1 km2 above 2300 m) and corresponding woodland area are small. In addition, it is relatively close to two higher mountains (Huachuca Mountains in the United States, and Sierra de los Ajos, the highest island in Mexico) that may act as potential source populations of pines. Birds are known to disperse the seeds of certain pines species and two species that have been found in the San José, *Pinus discolor and P. strobiformis* belong to the strobi and cembroides groups of pines that have large and wingless seeds potentially dispersed by birds

(Lanner 1998). Our recent fieldwork, however, failed to document *P. strobiformis* (or *P. chihuahuana*) in the San José that were originally found in 1893 by Mearns (1907; specimens examined by us). These species may now be locally extirpated due to greater susceptibility of small populations to stochastic extinctions as a continuing process, i.e. the few *P. strobiformis* individuals Mearns found near the summit removed by fire.

Varying adaptive strategies of Sky Island pines might explain their present distributions. One pine of the CP-RM element continues across the Sky Islands into the northern SMO, *Pinus ponderosa* var. *scopulorum*; it belongs to a widespread and adaptable "ponderosae" complex with varieties (and species) that range from British Colombia to central Mexico. Pleistocene and early Holocene records are only in Arizona; its range expanded northward during the last 8000 years just as another northern element *P. edulis* did from refugia in the southwestern United States (Lanner and Van Devender 1998). Two pines of the Madrean element that range across 23 Sky Islands and reach the edge of the Colorado Plateau can survive at lower elevations—*P. discolor* as low as 1150 m, and *P. chihuahuana*, on the fringe of the Sky Islands as low as 1310 m—and exhibit better drought tolerance than other pines. *P. engelmannii* is the dominant pine in the SMO, but also occurs on the edge of the SMO and in lower Sky Islands where populations are small, yet does not occur into the northern Sky Islands. *P. arizonica*, widespread in the higher SMO, mostly occurs on mesic N-facing slopes, or canyon bottoms of the higher Sky Islands including the highest northern ones. *P. strobiformis*, the most widespread and highest elevation of any Madrean element pine in the Southwestern United States, is potentially bird-dispersed (by corvids and thick-billed parrots). The northernmost populations of *P. yecorensis* in the Sierra Bacadéhuachi, and adjacent Sierra Huachinera of the SMO, are small and perhaps cold limited; farther south the species is more widespread on the lower Pacific slope of the SMO and borders Tropical Deciduous Forest around latitude 28°N.

None of the *Pinus* in the Madrean Sky Islands of Mexico or the United States have any federal or state conservation status, although limited protected areas exist as reserves (e.g. Ajos-Bavispe, Ramsey Canyon, Saguaro National Park), have controlled access (e.g. Animas Mountains, private), or are managed by the U.S. Forest Service. Disturbance events have altered pine forests at large scales across the Sky Islands (increased fires associated with human activities, insect outbreaks and drought). In smaller ranges where pines occur in tiny isolated populations, these disturbance events are affecting pine diversity and distribution, e.g., a tiny population of *P. engelmannii* on privately managed land in the Sierra San Antonio may have less then 20 individuals at present, with many recent snags that have succumbed to drought in the past 10 years. Similarly, *Pinus engelmannii* in the Sierra Cíbuta, the westernmost outpost for pines in the Sky Islands of Sonora, are in serious decline and many patches of pines have been lost in the last decade. Although marked as present on our list, such pines can be rare, e.g. only a single *P. edulis* was recorded from the Pinaleño Mountains (Jim Malusa, personal observation 1985). Other areas may be under sampled, or less explored, such as in Sierra Enmedio, Chihuahua, where no collections exist for a high mountain bound to support at least one pine species, and in the Dragoon Mountains, Arizona, with only one pine species recorded. The spread of some introduced pines should also be monitored, such as the Eurasian *Pinus sylvestris* that is locally introduced on private lands in the Sierra de los Ajos, Sonora. Given threats to small isolated populations on mountain tops and a rapidly warming and drying climate in the region, efforts to document and monitor the distribution and spatial extent of pine forests across the Sky Islands is critical for conservation.

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