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Verrier, James T.

Mulder, Kenneth

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The distribution and abiotic drivers of subtropical plant taxa in the southwestern U.S. sky island region: identifying hotspots of conservation significance with an aggregation of peripheral species

James T. Verrier^{1*}  and Kenneth Mulder² 

¹School of Plant Sciences, University of Arizona, Tucson, AZ, USA;

²Department of Mathematics and Statistics, Mount Holyoke College, South Hadley, MA, USA.

* Correspondence: J.T. Verrier, jverrier@arizona.edu

Abstract

A contributing element of the exceptional plant biodiversity of the Arizona-New Mexico sky islands is the numerous southern taxa at their northern extent, yet the local distribution and drivers of subtropical plant richness have not been delineated. We assess the proportion of subtropical richness (*PSR*) in sky islands as the ratio of subtropical taxa to total species richness. We (1) identified 284 subtropical vascular plant species at or near their northern range in 24 sky islands, (2) calculated *PSR* for each sky island, (3) quantified spatial patterns of *PSR* and subtropical beta diversity, (4) determined regional hotspots of *PSR*, and (5) analyzed independent eight variables as potential drivers of *PSR* and subtropical species turnover. Sky islands with the highest *PSR* occur in the southwestern portion of the region close to the international border. Four predictor variables (ordered by significance) strongly correlate with *PSR*: minimum winter temperature, monsoon season precipitation, area, and latitude. The primary subtropical hotspot occurs mostly within Santa Cruz County (southeastern Arizona), representing the largest regional concentration of rare subtropical taxa. We determined three primary clusters of species co-occurrence with a strong longitudinal trend driving subtropical beta diversity. Nearly half of subtropical taxa are regionally rare or vulnerable, illustrating the potential value of assessing regional peripheral plant taxa to discern hotspots of ecological significance. The sky islands of Santa Cruz County represent a unique botanical hotspot with exceptional subtropical richness and rarity. Understanding regional drivers of subtropical influences helps forecast potential responses to global change, while strengthening conservation strategies that minimize future losses of biodiversity.

Highlights

- Subtropical plant distribution in the southwestern U.S. sky island region is primarily predicted by the extent of minimum winter temperature and warm-season precipitation.
- Our results demonstrate that approximately 13.5% of the estimated regional flora is represented by peripheral plant taxa at or near their northern geographic distribution.
- We determined three sky island clusters of subtropical biotic similarity, which demonstrate a strong longitudinal progression from west to east. While warmer minimum winter temperature is a significant driver of the beta diversity of western sky islands surrounded by Sonoran Desert, the biotic similarity of eastern sky islands clustered along the Chihuahuan Desert was predicted by colder minimum winter temperature.
- The primary subtropical hotspot in Santa Cruz County, Arizona is a significant repository of rare and vulnerable species, containing 77% of all regionally rare subtropical taxa and nearly 87% of all regional subtropical taxa.
- Evaluating aggregations of peripheral populations may be especially valuable at biogeographic crossroads to delineate hotspots of conservation and ecological significance.

Keywords: abiotic drivers, Arizona sky islands, conservation, minimum winter temperature, peripheral populations, rarity hotspots, regional ecotones, sky islands, subtropical distribution.

Introduction

The Arizona-New Mexico sky islands are known for supporting many plant taxa at their northern range (Felger and Wilson 1995, Verrier 2018); however, the distribution and drivers of these peripheral species with southern affinities have not been investigated. Located in southeastern Arizona and southwestern New Mexico, this area is the northern extent of the greater Madrean Archipelago (Fig. 1). Sky islands are isolated mountain ranges separated by broad lowlands or valleys (McCormack et al. 2009, Carnahan 2020); these unique mountains are also defined by a vertical diversity of plant communities varying from lower desert or grassland to higher-elevation forest assemblages. Although delineated by an arbitrary political boundary on its southern edge (the U.S.-Mexico border), the region's northwest-southeast trending geology facilitates sky island biodiversity and ecological flows, encouraging a northern migration of subtropical taxa from tropical Central America to the Rocky Mountains (Drewes 1981, Warshall 1995b). Here, floristic influences intersect at the convergence of five physiographic provinces: Chihuahuan Desert, Neotropics, Rocky Mountains, Sierra Madre, and Sonoran Desert (Van Devender et al. 2013); it is the only global sky island complex spanning a subtropical and temperate distribution, which defines its unique floral character (Warshall 1995a).

The biological richness of the Arizona-New Mexico sky island region is largely due to geographic location, climate, and complex geology. An eclectic mixture of desert, grassland, and montane species commingle with plants of subtropical affinity in the sky islands. This region experiences a bimodal annual pattern, the winter El Niño Southern Oscillation and the summer North American Monsoon (Adams and Comrie 1997, Alexander et al. 2002). A combination of warm temperatures and monsoon precipitation fosters a rich assemblage of animals, plants, and invertebrates in the region (Buchmann 1995, Bowers and McLaughlin 1996, Koprowski et al. 2005). While Arizona sky islands occupy less than 3% of the state's area, they contain approximately 53% of its total vascular plant richness (McLaughlin 1995, Stein 2002, Canotia n.d.). Additionally, an extensive elevational gradient of approximately 2500 meters and diverse topography contribute to the distinct biological composition of the sky islands (Coblentz and Ritters 2005).

The southwestern U.S. sky islands occur along a biogeographic crossroads of physiographic regions and host a sizable number of subtropical plant taxa at their northern range. Although abiotic and biotic factors shape the distribution of species, plants are indicators of climatic conditions (Whittaker 1967, MacArthur 1972, Mott 2010, Brunbjerg et al. 2018), which may be explained by a diminished quantity or quality of appropriate habitat (Lee-Yaw et al. 2016, de Medeiros et al. 2018). Temperature and precipitation dynamics are significant drivers of the range limits of peripheral plant taxa. Temperature extremes strongly influence the geographic distribution of subtropical species (Sage et al. 1999, Sommer et al. 2018,

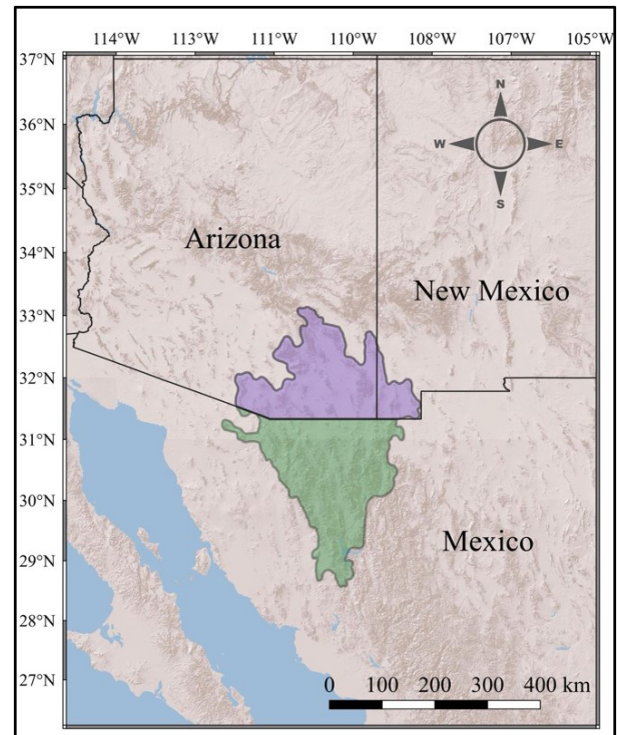


Figure 1. The Madrean Archipelago of the southwestern United States and northwestern Mexico. The purple shading represents the southwestern U.S. sky island region, and the green shading shows the Mexican portion of the Madrean Archipelago.

Zhang et al. 2020), and the cold tolerance of subtropical plants can correspond with range extent, latitudinal gradient, and ecoregional boundaries (Shreve 1914, Duker et al. 2015, Wen et al. 2018). Augmented warm-weather (monsoon) precipitation also characterizes humid subtropical habitats (Trewartha and Horn 1980).

Species at their geographic extremes often have local rarity designations, and numerous researchers have advocated for increased conservation of some peripheral populations (Lesica and Allendorf 1995, Nielsen et al. 2001, Bunnell et al. 2004, Channell 2005, Gibson et al. 2009, Rehm et al. 2015); however, this subject is contentious. A policy dilemma is that peripheral species with regional rare listings are usually globally secure (Caissy et al. 2020). As resources to implement conservation policies are limited, Peterson (2000) argued that protecting peripheral species detracts from more valuable preservation efforts. Although marginal populations are known to be less genetically diverse or genetically bottlenecked in extreme cases (Soule 1973, Lesica and Allendorf 1995, Frankham 1996, Weidema et al. 1996, Gao and Gao 2016, Langin et al. 2017), unique genetic variation or adaptations in peripheral populations could benefit species conservation efforts (Lomolino and Channell 1995, 1998, Lammi et al. 1999, Hardie and Hutchings 2010). Harsh environmental conditions and reduced habitat quality along the periphery can also augment resiliency (Gaston 2003), a vital adaptation during the

rapid rate of modern climatic change (Gibson et al. 2009, Hardie and Hutchings 2010, Rehm et al. 2015). Rare and vulnerable species are particularly sensitive to global change as they occupy specialized habitat, which is threatened by recent losses of sky island habitat and projections of significant montane habitat loss over the next decades (Villarreal et al. 2019, Yanahan and Moore 2019).

In this study, we utilize a large aggregation of northern peripheral plant taxa to discern the local distribution and drivers of sky island subtropical richness. Since bigger sky islands may contain more subtropical taxa than smaller sky islands, we investigate the proportion of subtropical richness (*PSR*), defined as the ratio of subtropical taxa to total species richness within each sky island flora. An additional goal is to analyze shared patterns of subtropical vegetative composition between sky islands. Finally, we determine the highest local density of regional subtropical influence (hotspots), which are likely ecologically significant due to higher concentrations of peripheral species with rarity designations. Discerning species distribution and richness are critical to identifying high-value concentrations of rare species and implementing ecological preservation strategies in the Anthropocene.

Materials & Methods

Study area

The study area occurs within the Madrean Archipelago (Fig. 1) physiographic region in Arizona and New Mexico (U.S. Environmental Protection Agency 2013, Griffith et al. 2014). Different authors

have proposed varied definitions for the Madrean sky islands based upon the extent of vegetative association diversity, all of which include a specific woodland association. Marshall (1957) described the greatest richness of sky island plant communities and identified pine-oak woodland (excluding pinyons) as the defining habitat; only nine ranges qualify for this description. Bezy & Cole (2014) determined sky islands based on the occurrence of Madrean Evergreen Woodland (oak-juniper-pine woodland) as defined by Brown (2014), but recognized four additional ranges stretching northward into central Arizona. Oak woodland was utilized by Deyo et al. (2013) and Moore et al. (2013), who employed the broadest interpretation of regional sky islands. Moore et al. (2013) also recognized two additional sky islands north of the classically-defined Madrean Archipelago (Griffith et al. 2014). We recognize oak woodland areas determined by Deyo et al. (2013), but utilize an intermediate sky island classification identified by oak-pine woodland, or oak assemblages including any pine species. Online herbarium records on the Southwest Environmental Information Network (SEINet) (SEINet n.d.) were examined to verify the presence of pine species for our sky island determinations. We identified a total of 24 sky islands in the study area utilizing this criterion (Fig. 2); three ranges previously classified as sky islands by Deyo et al. (2013) are excluded due to a lack of oak-pine woodland (Alamo Hueco, Perilla, and Tortolita). However, we recognize two sky islands as clusters of several adjacent mountain ranges that are not clearly differentiated from each other, which is consistent with Deyo et al. (2013); Atascosa, Pajarito,

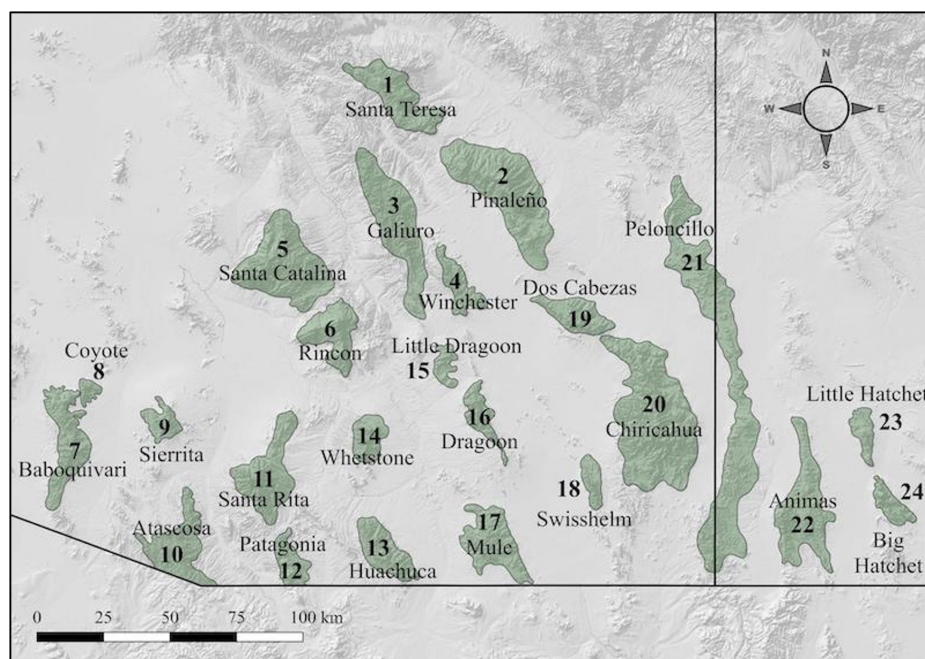


Figure 2. The study area includes 24 sky islands in southeastern Arizona and southwestern New Mexico, representing the northern portion of the Madrean Archipelago. Sky islands were determined by those containing oak-pine woodland, or oak assemblages including any pine species.

and Tumacacori are defined here as Atascosa, while Baboquivari includes nearby Quinlan.

Although three sky islands share a geographic distribution in both the United States and Mexico (Atascosa, Huachuca, and Peloncillo), we only examine botanical specimens and abiotic data from the U.S. portion of these mountain ranges. In addition to significantly less climate, geological, and botanical collection data from the Mexican border ranges, our primary interest is providing ecological and conservation insight for land management agencies in the southwestern U.S. sky island region.

Sky island subtropical plants

Plants identified in the sky island region were determined to be subtropical if they met the following conditions: a) those with a Mexican distribution that reach their northern range in Arizona-New Mexico sky islands and b) southern taxa with only a handful of ephemeral populations north of the sky islands (ephemeral peripheral hereafter). We identified subtropical taxa by reviewing online herbarium records on SEINet (SEINet n.d.) and all published floras (Wagner 1977, Toolin et al. 1979, Wentworth 1982, Bowers and McLaughlin 1987, Johnson 1988, McLaughlin and Bowers 1990, McLaughlin 1993, Bennett et al. 1996, Bowers and McLaughlin 1996, Buegge 2001, McLaughlin and McClaran 2004, Verrier 2018). A total of 82,507 records were processed from an assortment of regional herbaria through the SEINet database. Range distributions for each sky island plant taxa were estimated with the SEINet map function to determine those qualifying as subtropical taxa (Fig. S1).

The SEINet database was accessed to download all sky island herbarium records by searching the terms “mountains” and “mts” for each range or combination of ranges (i.e., Atascosa Highlands). Search criteria for Swisshelm also included “Leslie Canyon, Cochise County.” Due to the low number of collections from Little Dagoon, records from the bordering Texas Canyon area were included in this range. We examined records that were potentially problematic by examining the collection label to clarify the locale data. Questionable records represented by a single and highly disjunct specimen were discarded unless made by a well-known collector. Collections represented solely by historical relicts not known to be regionally extant were excluded.

Botanical field determinations were also made from one highly under-collected sky island (Sierrita), which is located between two sky islands with numerous subtropical plant taxa, Baboquivari and Santa Rita (McLaughlin and Bowers 1990, Austin 2010). Species occurrences in Sierrita seemed important to help us better understand subtropical plant distribution in the western part of our study region. We undertook nine days of fieldwork in Fall 2021 across this mountain range in an assortment of geologic substrates, habitats, and elevational gradients. All plant taxa not previously known to the flora of Sierrita were identified in the field with a hand lens and electronic dichotomous keys to avoid a subtropical collection bias.

We also identified the rarity status for all regional subtropical plants. Our rarity classification includes taxa with rare, vulnerable, endangered, and species of concern designations. For this process, we utilized NatureServe (NatureServe 2022) state conservation rankings, the Arizona Game and Fish Department Heritage Data Management System (Arizona Game and Fish Department 2021), the New Mexico Conservation Information System (New Mexico Natural Heritage n.d.), and the New Mexico Rare Plant List (New Mexico Rare Plant Technical Council 1999). Species ranked by NatureServe as S1 (critically imperiled), S2 (imperiled), or S3 (vulnerable) were included in our rarity determinations. We classified taxa with an intermediate rarity status of S1/S2 as S2 and S2/S3 as S3.

We calculated sky island *PSR* by dividing subtropical plant richness by total species richness for each sky island. Since only eight sky islands have published floras, we also generated the approximate total taxa for the remaining 16 ranges from existing herbaria records, which were edited to correct taxonomic synonymy and to remove questionable records.

Predictor variables

We examined eight independent variables as potential drivers of *PSR* (Fig. 3), which were selected as we hypothesize factors that drive overall diversity might also influence *PSR*. Three climate variables were included due to their strong relationship with subtropical taxa (Shreve 1914, Mott 2010, Wen et al. 2018): minimum winter temperature (T_{min}), and two measures of precipitation, monsoon season precipitation (P_{mon}) and annual precipitation (P_{tot}). Elevational range (E , the difference between minimum and maximum elevation) was also chosen due to its known relationship with species richness and increased beta diversity (Trigas et al. 2013). While latitude (Lat) correlates with biodiversity, we also include longitude (Lon) due to regional temperature influences from the Sonoran (west) and Chihuahuan (east) deserts (Schmidt 1986, Weiss and Overpeck 2005). The log-transformed area (km^2) of each sky island (lnA) was also examined as larger ranges likely host greater species diversity. Finally, geological richness (G) was chosen as a key component of geodiversity, a correlate of plant species richness (Gray 2013, Hjort et al. 2015). These variables were also considered as possible drivers of sky island community similarity (beta diversity or species turnover). Values for these variables were calculated using QGIS 3.16.13.

Our measure of geological richness is the sum of lithographic (unique geological substrates), chronostratigraphic (geological time periods), and mineral units for each range. We downloaded shapefiles from the United States Geological Services (USGS) Geological Map Database of the Conterminous United States and USGS Mineral Resource Data System (U.S. Department of Agriculture 2021) and conducted a geological literature review for all 24 sky islands (Hayes and Landis 1964, Young 1969, Hayes 1970, Drewes et al. 1972, Sousa 1980, Thorman 1981,

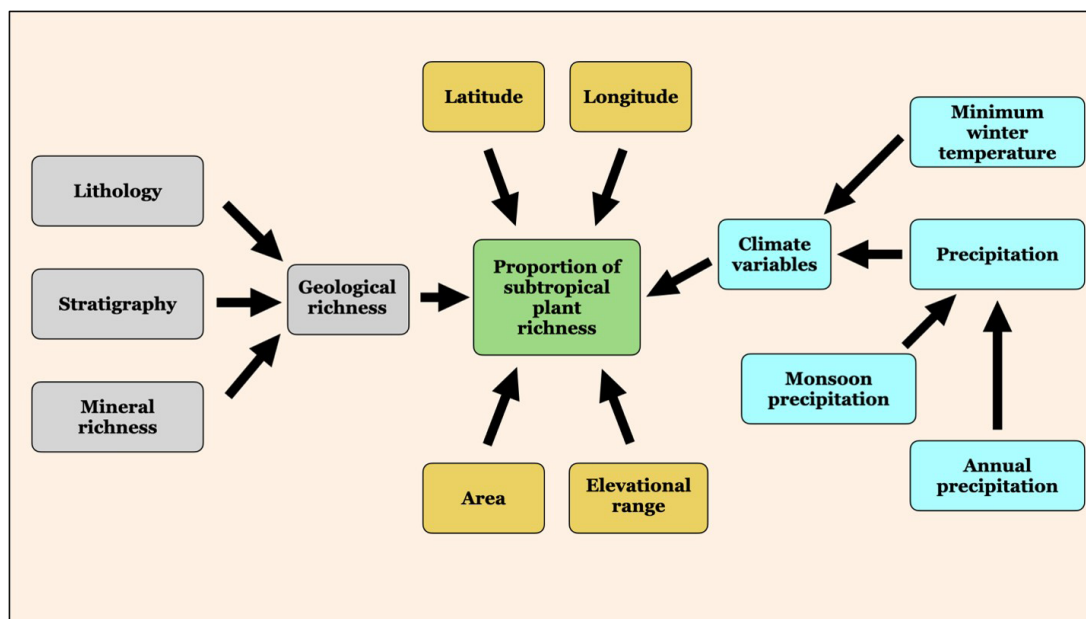


Figure 3. Modeled drivers of the proportion of subtropical plant richness (PSR) in the Arizona-New Mexico sky islands. Eight potential variables were selected, including three climate variables. Geological richness is shown here as the sum of three metrics.

Bykerk-Kauffman 1983, Wrucke and Armstrong 1984, Currier 1985, Hauck 1985, Mark 1985, Davis et al. 1987, Dickinson et al. 1987, Spencer 1993, Armstrong and Brown 1994, Huckelberry 1996, Force 1997, Dickinson 1998, Houser 2005, Busby and Bassett 2007, Bykerk-Kauffman 2008, Graham 2010, Davis et al. 2011, Rasmussen et al. 2012, Graybeal et al. 2015, Borel 2018, Johnson et al. 2018). As soil surveys are absent from 37% of the study area (U.S. Department of Agriculture 2021), it was not possible to calculate a geodiversity index (Serrano and Ruiz-Flaño 2007). However, we investigate a possible relationship between *PSR* and geological richness.

Computer-modeled gridded climate datasets offer a readily available and systematic resource to evaluate warm macroclimates and seasonal precipitation in the region. PRISM (Parameter-elevation Regressions on Independent Slopes Models) provides relatively accurate climate data based upon point station data at intervals across the conterminous United States, although several overestimations occur in mountainous terrain, including increased cold bias in all seasons and exaggerated precipitation (Ahn et al. 2014, Daly et al. 2017, Strachan and Daly 2017, PRISM Climate Group 2021). Station coverage is relatively good for PRISM from 1981 to present, which affords somewhat stable long-term climate data for the recommended standard of thirty years of consecutive climate data (Daly et al. 1994, Daly et al. 2008, Parra and Monahan 2008, World Meteorological Organization 2009, Daly et al. 2017).

We obtained climate data from PRISM 30-year averages (1981–2010) at 800 m resolution. The mean minimum temperature for the three coldest winter months (December, January, and February) was used to generate T_{min} . Monsoon precipitation was calculated

from July and August totals. Although the North American monsoon is arbitrarily considered active through September 15th (Crimmins 2006), moisture occurring during September is often associated with cooler temperatures and comes at a time when many subtropical taxa are entering seasonal dormancy. Mean climatic averages for each sky island were calculated with zonal statistics in a GIS.

Statistical analyses

Modeling the proportion of subtropical richness

We chose eight independent variables as possible factors in determining the proportion of subtropical species richness: E , $\ln A$, Lat , Lon , G , T_{min} , P_{mon} , and P_{tot} . Predictor variables were standardized (mean centered and scaled) and used to fit a binomial generalized linear model with the logistic link function. Variables were selected using a stepwise selection procedure (step procedure in R) using the Bayesian Information Criterion (BIC) to sequentially filter out predictor variables that did not improve the model. BIC is a more parsimonious criterion than Akaike's Information Criterion, thereby producing a more regulated model, which seemed warranted given the sample size and number of predictor variables. Selected variables were assessed for multicollinearity. We further assessed the possibility for Type-I errors associated with the stepwise selection procedure by using a permutation test with 5000 replicates and a parametric randomization test to assess the probability of the observed difference in BIC under the assumption of no relationship between the predictor variables and the observed proportions.

For each identified predictor variable in the best model, we used the difference in BIC between the best model and the best model minus the variable in question to assess the evidence in favor of that variable. Following Jones et al. (2001), we determined that a difference in BIC greater than five indicated very strong evidence that the variable was a significant factor in determining *PSR* and a difference between three and five indicated strong evidence. Coefficients for each predictor variable in the best model were estimated using the GLM function in R. To calculate a 90% confidence interval for each coefficient, we generated 20,000 bootstrapped samples, calculated coefficients for each sample, and determined the 5th and 95th percentile for each set of coefficients.

Modeling and predicting species composition similarity

All calculations in this section were performed using the software Primer-e v7. Presence data for 284 subtropical species were used to create a similarity matrix for the 24 sample locations using the Bray-Curtis similarity index (Bray and Curtis 1957) (Fig. S1), which is identical to the Sorensen-Dice coefficient for binary data. Given two locations, X and Y, where X equals the number of species the two sites have in common while Y equal the number of species in site X and Y, respectively. Non-metric multidimensional scaling (NMDS) was performed to create a two-dimensional representation of the relative distances between sample locations. A permutation-based hierarchical clustering algorithm with 10,000 replications was used to search for meaningful groupings of the locations based on the species present at each site, and the Similarity Profile (SIMPROF) test (Clarke et al. 2008) was used to test for the significance of the observed differences (Type-I error rate set at 5%). SIMPROF is a permutation *a posteriori* test that does not require an *a priori* hypothesis. It is well suited to identifying significant groupings in unstructured species presence data that correspond to meaningful ecological communities.

Abiotic covariates and drivers of community similarity

Three steps were taken to search for abiotic drivers of community similarity using the eight independent variables used to model *PSR*. The independent variables were again standardized (mean centered and scaled). To look for correlations between abiotic variables and community assemblage, we used the BEST routine, which searches for the most explanatory subset of abiotic variables (Clarke et al. 2008). The Global BEST test was applied to the result to assess the significance of the findings. Global BEST cannot determine the significance of any single predictor variable, but it does provide a reliable, post-hoc significance test of the overall result looking for a relationship between the given set of abiotic variables and the similarity between each pair of communities.

Using the identified variables from the BEST routine, we used the LINKTREE procedure to look

for significant thresholds in the predictor variables to categorize the locations based on biotic similarity. LINKTREE is a constrained binary divisive algorithm that seeks to cluster samples based on breakpoints in quantitative variables. These breakpoints were added to the NMDS plot to graphically represent how these thresholds corresponded with resemblance based on species assemblage.

Finally, we wanted to graphically represent different abiotic variables and their relationship to the difference and similarities between plant communities. To this end, we divided each variable into five categories based on normalized quintiles. These categories were plotted on the NMDS representation. We also used the five categories as factors for an Analysis of Similarity (ANOSIM), a permutation test for a significant relationship between the factors and the Bray-Curtis similarity matrix (Clarke 1993).

Sky island subtropical plants

Sky islands with the highest regional *PSR* were used to identify hotspots of subtropical influence. Hotspots are represented as either individual sky islands or clusters of adjacent sky islands, which were determined through statistically significant overlap of subtropical species based upon the results of the Bray-Curtis biotic similarity analysis. For each hotspot cluster, *PSR* was calculated by averaging the *PSR* for all sky islands within the cluster.

The number of rare subtropical taxa was also determined for each hotspot to provide potential conservation insight. We calculated (a) the percentage of rarity for each hotspot, represented by the ratio of rare subtropical taxa within the hotspot to all regionally rare subtropical taxa and (b) the proportion of subtropical taxa in relation to the total number of regional subtropical species.

Results

A significant number of subtropical plant taxa were determined from the study area, representing approximately 13.5% of estimated regional floristic richness. The highest concentrations of *PSR* occurred in the southwest portion of the region close to the international border. We identified 284 subtropical peripheral taxa from the known regional flora of ~2100 taxa (McLaughlin 1995), encompassing 60 families and 195 genera (Fig. S2). In this group, there were 191 taxa at their northern extent (67%) and 93 ephemeral periphery taxa (33%) (with a few outliers north of the study region). Sixty-five subtropical taxa are annual (~23%) and 219 are perennial (~77%). Plant families with the greatest number of subtropical taxa are Fabaceae (51), Asteraceae (48), Poaceae (18), Apocynaceae (15), Malvaceae (11), and Convolvulaceae (10). Genera with the highest number of subtropical plant taxa include *Dalea*, *Asclepias*, *Desmodium*, *Muhlenbergia*, and *Ipomoea*, respectively with 8, 7, 7, 7, and 5 taxa each. We identified a clear break in *PSR* for six sky islands with the highest *PSR* (equal to or greater than 16.0%), while all other sky islands had

a *PSR* equal to or less than 13.5%. Sky islands with the highest *PSR* were Patagonia (23.9%), Atascosa (19.0%), Santa Rita (16.4%), Mule (16.3%), Huachuca (16.1%), and Baboquivari (16.0%) (Table 1) (Fig. 4).

During our fieldwork in Sierrita, we identified an additional 51 subtropical taxa, increasing the known number in that sky island to 60. The vascular flora of Sierrita was also expanded from the previously known total of 121 to 443 plant species.

A total of 135 subtropical taxa are rare or vulnerable, representing 47.5% of regional subtropical plant species. This includes one endangered species, one species of concern, 35 very rare taxa, 41 rare taxa, 45 vulnerable taxa, and 12 rare taxa without a recognized conservation status. Only six subtropical taxa had rare designations in New Mexico; while all six occur in Arizona sky islands, four of these taxa lack a rarity status in Arizona.

Statistical analyses

Abiotic drivers of *PSR*

Values of the response and predictor variables for the 24 samples are shown in Table 2. Sample statistics

for the eight predictor variables (used to standardize the variables) are shown at the bottom of Table 2.

Six predictor variables were identified as part of the best linear model for predicting the proportion of subtropical plant species. In order of significance, they are minimum winter temperature (T_{min}), monsoon season precipitation (P_{mon}), the log-transformed area ($\ln A$), geological richness (G), latitude (Lat), and elevational range (E). There was some observed collinearity between the elevational range and the log of the area ($r = 0.60$). Logistic coefficients for the standardized variables and the difference in BIC between the model with the variable and without the variable are reported in Table 3. Both the permutation test and the parametric randomization test showed the model to be highly significant, with no permutation out of 5000 replicates (for each test) having a greater difference in BIC than the observed difference (-313.8). Model fit was good; the correlation between observed and predicted *PSR* was $r = 0.933$.

Computed confidence intervals were consistent with the GLM coefficient estimates and the determination of significance using the difference in BIC in all cases

Table 1. The proportion of subtropical richness (*PSR*) in the southwestern U.S. sky island region. The number of subtropical plant taxa occurring in each range is also listed, along with the known species richness of plants. Sky islands without existing floras are designated with an asterisk.

No.	Sky island	Proportion of subtropical richness to flora	Subtropical indicator richness	Total known flora
12	Patagonia *	23.9%	129	540
10	Atascosa	19.0%	176	925
11	Santa Rita	16.4%	195	1,188
17	Mule *	16.3%	95	583
13	Huachuca	16.1%	160	994
7	Baboquivari *	16.0%	109	682
9	Sierrita *	13.5%	60	443
6	Rincon	12.0%	130	1,084
19	Dos Cabezas *	11.4%	23	202
20	Chiricahua	11.2%	141	1,261
21	Peloncillo *	10.4%	68	651
8	Coyote *	10.4%	50	479
14	Whetstone *	10.2%	46	453
16	Dragoon	10.1%	72	712
5	Santa Catalina	9.6%	130	1,360
18	Swisshelm *	9.3%	45	486
15	Little Dragoon *	7.6%	27	356
4	Winchester *	6.8%	10	146
3	Galiuro *	6.6%	42	637
22	Animas *	6.5%	41	632
2	Pinaleño	4.6%	39	844
1	Santa Teresa	4.2%	27	637
24	Big Hatchet *	4.1%	10	242
23	Little Hatchet *	3.6%	12	330

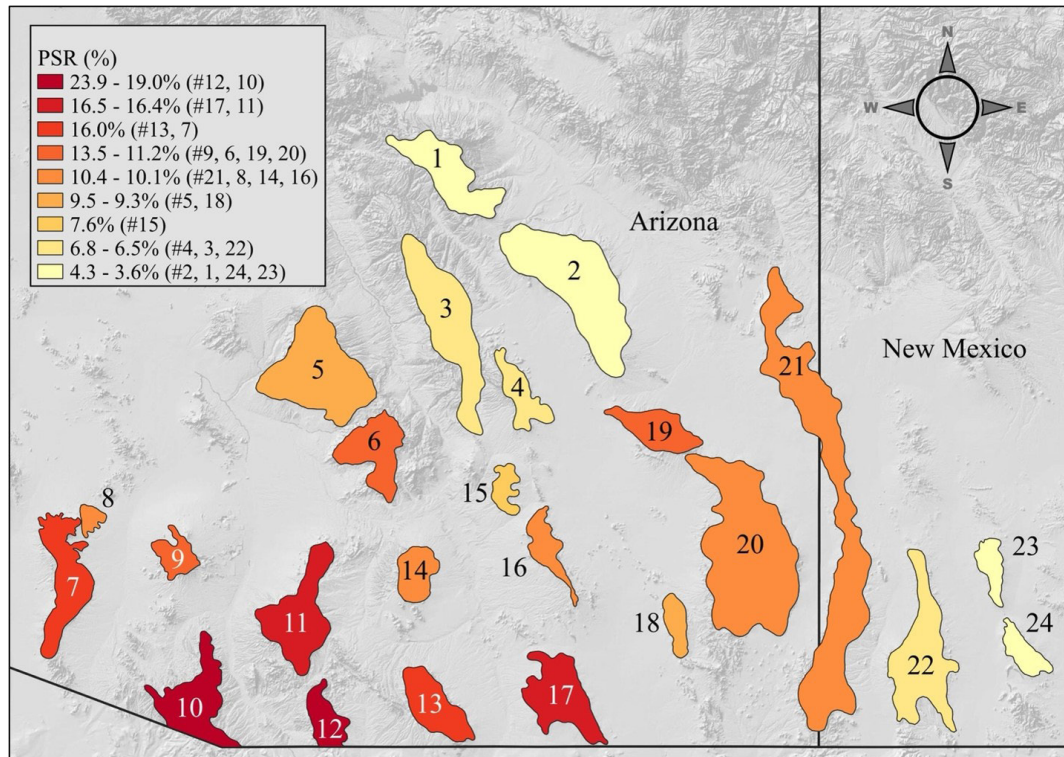


Figure 4. Regional heatmap of PSR in the southwestern U.S. sky island region. Darker red represents the highest proportion of subtropical richness, while yellow denotes the lowest extent of subtropical influence. The primary concentration of PSR occurs in the southwestern portion of the region in proximity to the international border.

Table 2. Independent variables of PSR in the Arizona-New Mexico sky islands: elevational range (*E*), area (*lnA*), latitude (*Lat*), longitude (*Lon*), geological richness (*G*), minimum winter temperature (T_{min}), monsoon season precipitation (Pr_{mon}), and annual precipitation (Pr_{tot}).

ID	Sky island	PSR	<i>E</i> (m)	<i>lnA</i> (km ²)	<i>Lat</i> (DD)	<i>Lon</i> (DD)	<i>G</i>	T_{min} (°C)	Pr_{mon} (mm)	Pr_{tot} (mm)
1	Santa Teresa	4.2%	1306	2.61	32.97	-110.30	96	-0.29	141	483
2	Pinaleño	4.5%	2222	2.95	32.65	-109.87	53	-0.93	183	520
3	Galiuro	6.6%	1197	2.82	32.55	-110.31	50	0.07	163	475
4	Winchester	6.8%	1007	2.28	32.34	-110.06	24	-0.57	187	541
5	Santa Catalina	9.6%	1965	2.87	32.41	-110.74	105	1.39	193	587
6	Rincon	12.0%	1636	2.52	32.18	-110.56	47	1.34	218	544
7	Baboquivari	16.0%	1479	2.61	31.82	-111.61	71	2.14	208	475
8	Coyote	10.4%	1078	1.74	31.99	-111.52	43	2.97	182	405
9	Sierrita	13.5%	842	2.12	31.88	-111.22	76	2.14	224	505
10	Atascosa	19.0%	910	2.62	31.44	-111.15	66	1.07	236	523
11	Santa Rita	16.4%	1810	2.67	31.71	-110.81	114	1.39	245	607
12	Patagonia	23.9%	944	2.23	31.41	-110.72	171	0.75	232	519
13	Huachuca	16.1%	1421	2.47	31.45	-110.35	70	-0.56	259	631
14	Whetstone	10.2%	987	2.26	31.83	-110.41	57	0.69	211	479
15	Little Dagoon	7.6%	716	1.99	32.08	-110.11	69	1.02	169	412
16	Dagoon	10.1%	863	2.21	31.91	-109.97	87	0.03	189	512
17	Mule	16.3%	932	2.62	31.48	-109.92	71	0.81	184	412
18	Swisshelm	9.3%	815	2.05	31.69	-109.53	44	-0.65	195	451
19	Dos Cabezas	11.4%	1318	2.39	32.24	-109.60	61	-1.00	174	439
20	Chiricahua	11.2%	1700	3.11	31.89	-109.29	109	-2.31	237	578
21	Peloncillo	10.4%	976	3.16	32.01	-109.04	189	-1.42	143	376
22	Animas	6.5%	1199	2.78	31.59	-110.70	126	-2.15	178	451
23	Little Hatchet	3.6%	653	2.08	31.85	-108.46	76	-2.20	147	344
24	Big Hatchet	4.1%	1198	2.13	31.61	-108.35	45	-2.62	180	410
	Mean	10.8%	1216	2.47	31.96	-110.11	80	0.05	195	487
	Standard deviation	5.2%	430	0.36	0.40	0.87	39	1.50	32	72

Table 3. Results for the logistic regression model for PSR for the six predictor variables identified by stepwise variable selection in the Arizona-New Mexico sky islands. The change in odds ratio shows the increase or decrease in the odds ratio of a plant species in the system being a subtropical species given a one-unit change in the predictor variable. shows the difference in the Bayesian Information Criterion between the model with and without that variable, and the last column shows the resulting evidence for this variable as a significant predictor.

Variable	Coefficient	90% Confidence	Change in odds ratio	Δ_{BIC}	Significance
Minimum winter temperature	0.2711	(0.183,0.366)	+31.1%	-70.99	Very strong
Monsoon precipitation	0.2362	(0.102,0.401)	+26.7%	-23.10	Very strong
Area (log)	0.1515	(0.047,0.290)	+16.3%	-9.27	Very strong
Geological richness	0.1079	(0.183,-0.059)	+11.4%	-8.92	Very strong
Latitude	-0.1897	(-0.324,-0.005)	-17.3%	-8.92	Very strong
Elevational range	-0.1311	(-0.268,0.000)	-12.3%	-4.71	Strong

except for geological richness (*G*). While the coefficient estimate for *G* is positive, 13.2% of bootstrapped coefficient estimates were negative, suggesting that the influence of *G* was not very uniform across sites, and a few sites may have skewed the coefficient estimate. Indeed, the data for *G* are skewed by two sites with very high geological indices, Patagonia and Peloncillo. Consequently, *G* should not be considered a significant linear predictor of *PSR*.

The change in odds ratio (Table 3) shows the change in the ratio of the probability of a species being subtropical to the probability of it not being subtropical ($\frac{p}{1-p}$, where p = proportion of subtropical species). Since the variables have been standardized, they can be interpreted as the result of a change of one standard deviation. Thus, a one standard deviation increase in T_{min} leads to a 31.1% increase in the odds ratio for any given species being a subtropical species.

Monsoon precipitation and the log of the area were all also positively correlated with the probability of a species being subtropical. Greater elevational range and greater latitude were all negatively correlated with the proportion of subtropical species.

Assessment of biotic similarity between sky islands

The two-dimensional NMDS representation of the similarity matrix is shown in Fig. 5. Stress is slightly above desirable levels at 0.14, but comparison with the 3D representation (not shown) which had a stress level of 0.08 did not show any significant differences. The results of the clustering algorithm are presented in two ways. Fig. 6 shows the cluster dendrogram. Solid lines represent a statistically significant difference between islands or clusters based on the SIMPROF test. Dashed lines represent indistinguishable clusters. Fig. 7 shows a map of the different sample regions shaded and coded to represent the different clusters. Similarity thresholds report the minimum level of Bray-Curtis similarity between sky islands in the same cluster.

The NMDS plot shows a tight clustering of seven sky islands— Atascosa, Chiricahua, Huachuca, Patagonia, Santa Catalina, Rincon, and Santa Rita. These seven, along with Baboquivari, Coyote, and Sierrita form the

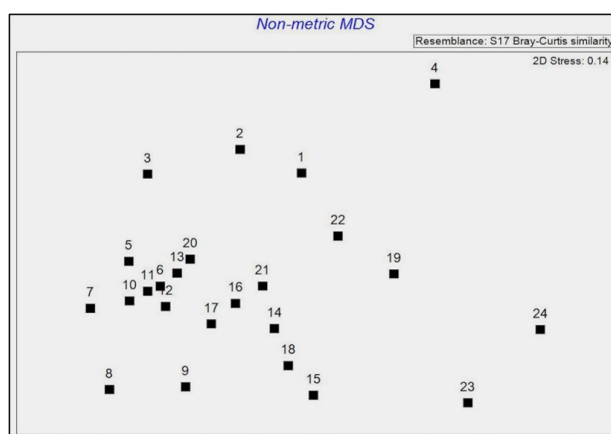


Figure 5. Plot of the first two dimensions of a non-metric multidimensional scaling representation of the Bray-Curtis similarity matrix seeking to match the ordination of distances between southwestern U.S. sky islands. In general, the farther two sites are from each other in the plot, the less their similarity. The two-dimensional stress (0.14) implies some inconsistencies between the plot and the similarity matrix.

main cluster (A) on the left side of the dendrogram in Fig. 6. The main cluster is somewhat clustered geographically in Fig. 7, except one outlier (Chiricahua) occurring significantly to the east. Dragoon, Mule, Peloncillo, Swisshelm, and Whetstone form another nearby cluster (B). Animas, Dos Cabezas, Little Hatchet, Pinaleño, and Santa Teresa form a loose cluster (C) separate from the others. Galiuro is in its own category, but it shares relatively equal biotic similarity with clusters A and B. Big Hatchet, Little Dragoon, and Winchester are on the far outskirts of the NMDS and do not belong to these three subtropical clusters. Big Hatchet and Little Dragoon are not significantly different from each other under the permutation test, which is likely because Big Hatchet bears little similarity to any other sky island except for Little Dragoon.

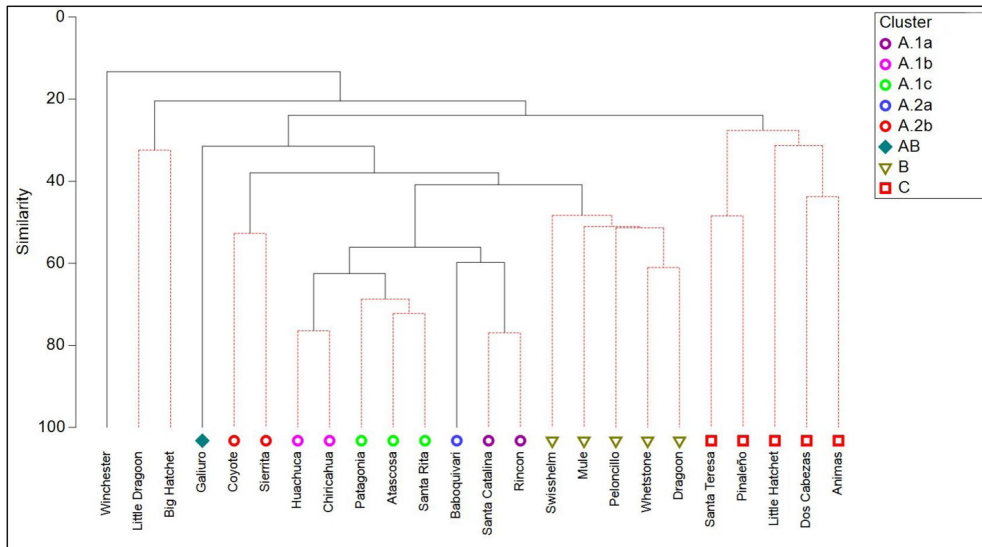


Figure 6. Dendrogram showing the results of the hierarchical clustering algorithm for subtropical biotic similarity in the Arizona-New Mexico sky islands. Dashed red lines show divisions that were not statistically significant based on the species present as determined by the SIMPROF routine. The vertical axis shows the percent similarity between samples connected at that level based on the average similarity between the samples on either side of the division. The symbols denote significant clusters and subclusters which are displayed in Fig. 7. Three samples were not assigned to clusters given their low similarity with all other samples.

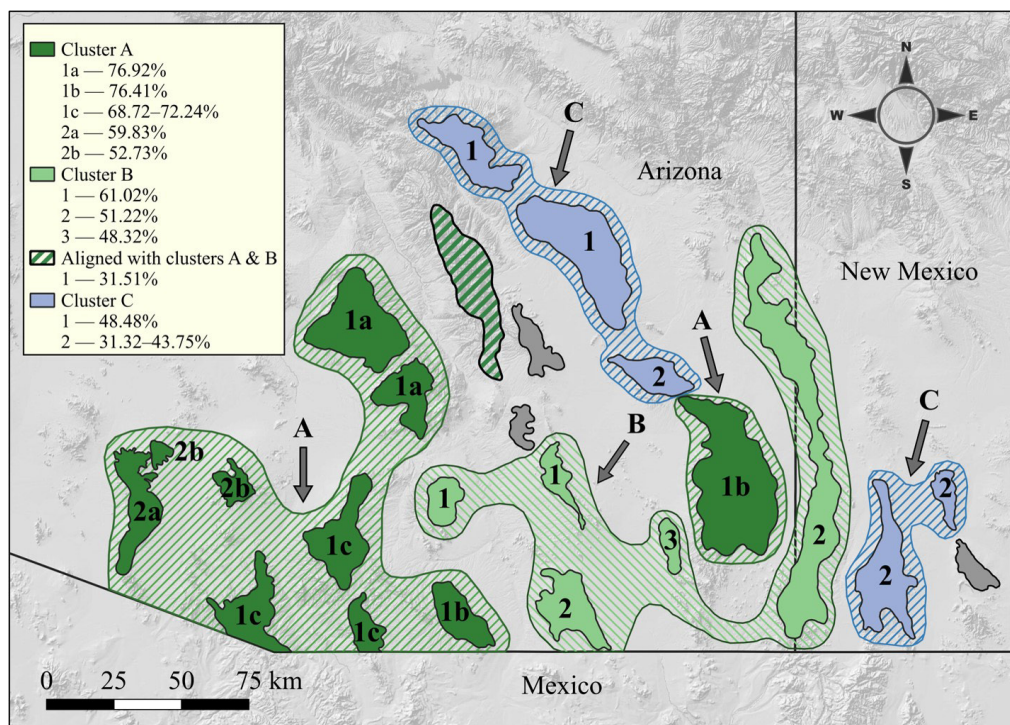


Figure 7. Map of the Arizona-New Mexico sky island region coded according to the results of the hierarchical clustering algorithm. Significant divisions based on the biotic similarity matrix are denoted by changes in color or number. Thresholds in similarity are shown in the key with the following exceptions: Galiuro (striped, green bars) is grouped with clusters A (dark green) and B (light green) but is its own category at a similarity level of 35.56%; clusters A and B have an average similarity of 30.97%, while Galiuro shares an average similarity with clusters A and B of 19.05%. Three sky islands (gray) that share the same coding were found to not be significantly different at the 5% level based on the post-hoc SIMPROF test, which were deemed to not have a high enough count of subtropical species for reliable categorization.

Abiotic drivers and covariates for biotic similarity

The BEST algorithm and associated permutation test for significance showed a strong and significant relationship between the species assemblage and the assessed abiotic variables (Spearman's $R = 0.472$, $p = 0.008$ based on 10^3 permutations). The most correlated subset of variables contained (in order of influence) longitude, latitude, minimum temperature, and the log of the area. Given the small number of species in Big Hatchet and Winchester, the BEST algorithm, the NMDS, and the clustering algorithms were recalculated with these sites removed. None of the outputs showed a significant change in the observed patterns of similarity between the other 22 sites. Given the linear nature of the BEST algorithm, potential outliers can influence which variables are selected and how strong the perceived relationship is. Removing these two sites increased the strength of the relationship

overall (Spearman's $R = 0.543$, $p = 0.001$), and annual precipitation and monsoon precipitation were added as significant factors, both being equally effective.

Fig. 8 shows the normalized quintiles for a subset of explanatory variables displayed sequentially on the NMDS plot. We also ran an ANOSIM test for each variable (as an unordered categorical variable), both with and without Winchester and Big Hatchet. The ANOSIM results reported are for all 24 sites. All six variables show a clear relationship to the similarity between sites, and the relationships with longitude and minimum winter temperature are particularly strong. Elevational range shows some clear patterns, but the patterns do not respect the order of the variable, suggesting a non-linear relationship. In general, the sites in the main cluster tend to be characterized (with some exceptions) as having high minimum winter temperatures, high annual precipitation, higher

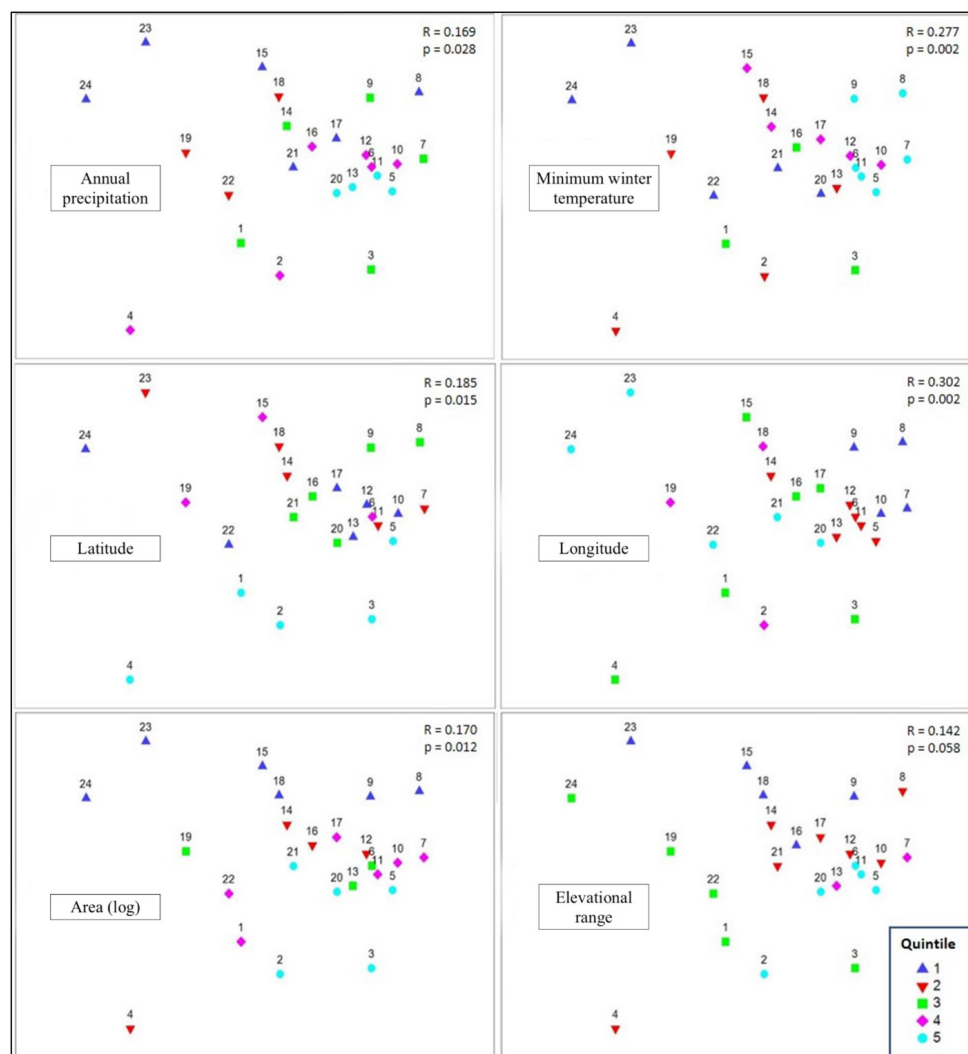


Figure 8. Display of normalized quintiles for six abiotic variables on the NMDS plot with one corresponding to the lowest normalized quintile (not necessarily the lowest quintile for the data) in the southwestern U.S. sky island region. Spearman's correlation coefficient and corresponding significance level (based on a permutation test with 10^4 replicates) for the ANOSIM test are shown in the upper left of each figure. Results are for each variable as an ordered categorical variable except for elevational range where the test for the ordered category was not significant ($R = 0.011$, $p = 0.381$).

elevational range, being larger in size, and lying to the southwest of the region.

There were some notable changes when the ANOSIM was run without Big Hatchet and Winchester. Spearman's R increased for longitude to 0.350 and for elevational range (unordered) to 0.254 ($p = 0.009$).

Results from the LINKTREE procedure are shown in Fig. 9. The procedure was run on longitude and latitude, which together had a Spearman's R = 0.467. Latitude and longitude accounted for the most meaningful divisions, and these divisions are apparent in Fig. 7. When the LINKTREE routine was run with temperature included, temperature was shown to be a determining factor in separating Baboquivari, Coyote, and Sierrita, all of which had an average minimum winter temperature more than one standard deviation above the mean, from the other sites. However, what is most apparent in Fig. 9 is the degree to which much of the clustering remains unexplained by the abiotic variables. Also, there seem to be some discrepancies between the LINKTREE divisions and the NMDS coordinatization. The LINKTREE procedure works directly with the resemblance matrix rather than the NMDS, and the relatively high level of stress for the

NMDS may be a partial explanation of the apparent differences.

Hotspots of conservation significance

Subtropical hotspots occurred in the southwest portion of the region, situated close to the international border. Based on the six sky islands with the highest regional *PSR*, we identified four hotspots of subtropical influence: three individual sky islands and one cluster containing three sky islands (Fig. 10). The regional epicenter of *PSR* was the Atascosa-Patagonia-Santa Rita cluster (average *PSR* of 19.7%), located primarily within Santa Cruz County. Two individual hotspots occurred along the border to the east of the primary hotspot: Mule (16.3% *PSR*) and Huachuca (16.1% *PSR*). The other individual hotspot was located on the extreme western edge of the region in Baboquivari (16.0% *PSR*).

All four hotspots comprised 92% of regional subtropical taxa and 83% of rare subtropical taxa. The primary subtropical hotspot (No. 1) contained 86% of regional subtropical taxa and 77% of rare subtropical taxa, while other hotspots contained significantly less taxa (Table 4).

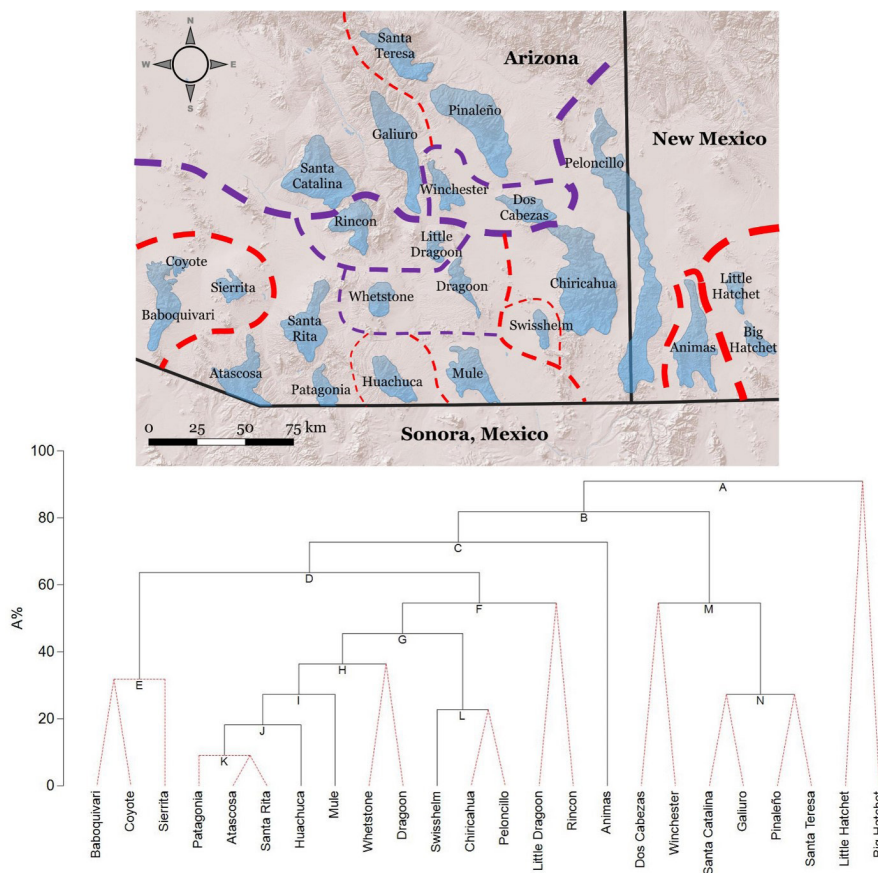


Figure 9. Significant breakpoints between Arizona-New Mexico sky islands based on the LINKTREE algorithm using longitude and latitude. Each dashed line in the top figure represents a statistically significant division (permutation test with 10^3 permutations) between sky islands based on subtropical plant assemblages. Line thickness is proportional to the species similarity within groups. Red lines indicate divisions based on longitude and purple lines indicate latitude. The lower figure shows the dendrogram based on the LINKTREE procedure.

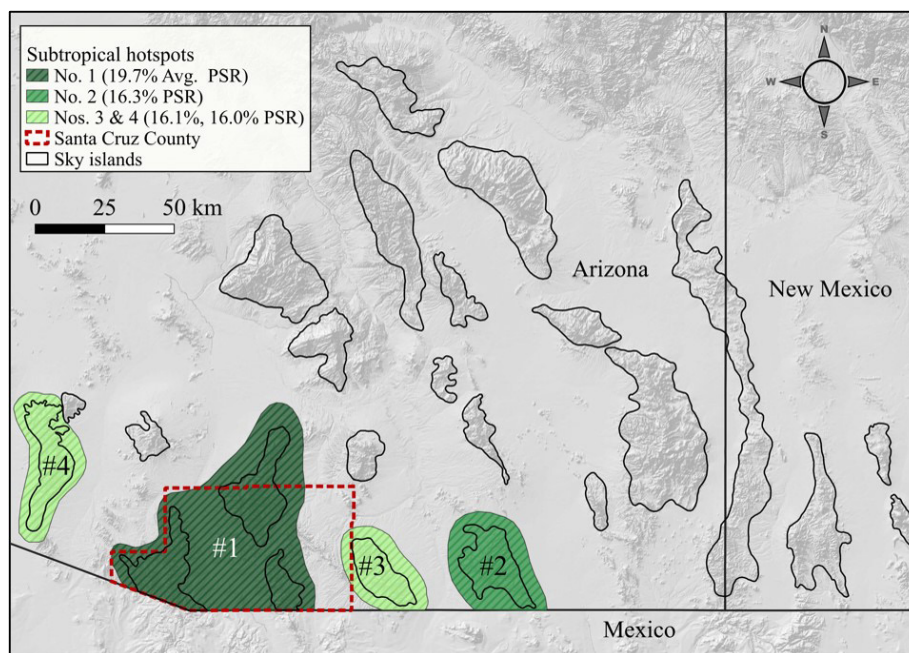


Figure 10. Subtropical hotspots in the Arizona-New Mexico sky island complex. Four subtropical hotspots are identified. The primary hotspot (#1) is a cluster of three sky islands, most of which occur within Santa Cruz County (represented as a red-dashed line).

Table 4. Species rarity and richness of subtropical hotspots in the southwestern U.S. sky island region. Rare percentage is the ratio of rare subtropical taxa to all regionally rare subtropical taxa (n=135); species richness represents all subtropical taxa present within a hotspot; richness percentage is the ratio of subtropical taxa present in a hotspot to regional subtropical taxa (n=284).

Hotspot	Combined <i>PSR</i>	Species richness	Richness %	Rare taxa	Rare %
No. 1 (10, 11, 12)	19.7%	246	86.6%	104	77.0%
No. 2 (17)	16.5%	96	33.8%	24	17.8%
No. 3 (13)	16.1%	160	56.3%	58	43.0%
No. 4 (7)	16.0%	109	38.4%	37	27.4%

Discussion

This study provides the first description of the distribution and abiotic drivers of subtropical plant influences in the Arizona-New Mexico sky islands. We show that the proportion of sky island subtropical richness is primarily a function of temperature and precipitation. Although we did not examine absolute subtropical species richness or diversity in each sky island, our results are consistent with previous studies demonstrating correlations between overall species richness and climate (Francis and Currie 2003, Hawkins et al. 2003, Moser et al. 2005, Vonlanthen et al. 2006, Hawkins et al. 2007). Since cold tolerance is well known to define subtropical range distributions (Duker et al. 2015, Sommer et al. 2018, Wen et al. 2018, Zhang et al. 2020), it is not surprising that minimum winter temperature exerted the most substantial influence on *PSR*. The seasonal timing of precipitation (monsoon) was a primary driver of *PSR*, which is congruent with increased warm-

season precipitation as a known characteristic of humid subtropical habitat (Trewartha and Horn 1980). The summer rainy season is also the primary active growing and reproductive period for many sky island subtropical plants, and a number of these taxa break dormancy in response to the onset of the monsoon and experience partial dormancy shortly after warm-weather precipitation ends. Annual precipitation was not a statistically significant subtropical correlate, further highlighting the strong relationship between subtropical plants and warm-weather precipitation.

Additional abiotic drivers of *PSR* with strong statistical correlations include area and latitude. Our results show that *PSR* corresponds with area, which conforms to expectations that more species will occur in larger areas (MacArthur and Wilson 1967, Rosenzweig 2010). However, we are unable to entirely explain the correlation between *PSR* and area, because complex dynamics can influence relationships between area and species (Lomolino 2001, Kallimanis et al.

2007). Additionally, sampling effort is known to affect species-area calculations (Chase et al. 2019), and botanical sampling differs between sky islands. We also demonstrate that latitude correlates with *PSR*. Here, sky island subtropical plant taxa approach the limit of their geographic distribution, and desirable habitat quickly diminishes across short distances at the periphery. In contrast, geological richness and elevational range demonstrated questionable validity as drivers of *PSR*. Elevational range had the weakest evidence for its association with *PSR* and exhibited collinearity with the area of a sky island.

The results from bootstrapping geological richness data infer that the influence of this variable is uneven across the sky island region. Patagonia and Peloncillo are both significant outliers with abnormally elevated geological indices, and this degree of richness is beyond what we would expect elsewhere in the region. Patagonia has the highest mineral richness of the sky islands, nearly three times greater than the average. The lithographic richness of Peloncillo is 3.5 times greater than the average, which may be partially explained by a latitudinal distance spanning nearly three-quarters of the study area. In this instance, our small sample size prevents the extrapolation of geological richness as a predictor of *PSR*. As soil data are absent for more than a third of the study area, we were unable to calculate for geodiversity, a well-known driver of biodiversity (Gray 2013, Hjort et al. 2015); however, if these data become available, an investigation of geodiversity could fill a knowledge gap regarding a potential correlation with sky island subtropical plant distribution and richness.

Our findings demonstrate the highest concentration of subtropical influences occur in a group of six sky islands along the southwestern portion of the region. Centered within this rich cluster of sky islands, the primary subtropical hotspot (No. 1 in Fig. 10) includes the adjacent Patagonia (23.9% *PSR*), Atascosa (19.0% *PSR*), and Santa Rita (16.4% *PSR*). Populations of all subtropical plant taxa in Santa Rita are represented in the southern half of the range, located within Santa Cruz County. Therefore, the epicenter of *PSR* can be classified as sky islands occurring in Santa Cruz County, despite the seemingly arbitrary nature of this political boundary. While Atascosa and Santa Rita are known to be exceptionally rich with subtropical plant taxa (Toolin et al. 1979, McLaughlin and Bowers 1990), Patagonia has not been botanically inventoried, despite possessing the highest regional *PSR*. Regardless of the political nature of the international border, the strongest subtropical plant influences occur close to the U.S.-Mexico border.

Sky island subtropical plant taxa are taxonomically represented by three dominant plant families: Fabaceae, Asteraceae, and Poaceae. As expected, our results show that the subset of species richness we examined (subtropical plants) are consistent with the well-documented phylogeographic bias of the region (Bowers and McLaughlin 1987, Bennett et al. 1996, Bowers and McLaughlin 1996, Verrier 2018).

Subtropical biotic similarity

Three sky island clusters (A, B, C) of subtropical biotic similarity were determined in a strong longitudinal progression from west to east (Fig. 7). Figs. 8 and 9 provide statistical support for longitude as a significant driver of regional biotic similarity. This west-east gradient in subtropical beta diversity is likely partially explained by the influence of minimum winter temperature, a positive correlate of longitude. In the three western-most sky islands surrounded by Sonoran Desert, warm winter minimum temperature is a significant driver of biotic similarity in Baboquivari, Coyote, and Sierrita. Conversely, cold minimum winter temperature predicts the biotic similarity on the eastern flank of the region in Peloncillo and Swisshelm, clustered along the Chihuahuan Desert. While the Sonoran Desert is the most subtropical and the hottest of the four North American deserts, the Chihuahuan Desert experiences extremely cold winter temperatures (Shreve and Wiggins 1964, Schmidt 1986, Turner et al. 1995, Weiss and Overpeck 2005). Although the primary cluster (A) is concentrated in the southwestern portion of the region, one outlier (Chiricahua) occurs to the east along the Arizona-New Mexico border. Chiricahua is the largest of five major sky islands with significant high elevation habitat. It receives the 3rd and 4th highest volume of monsoon and annual precipitation respectively and lies just north of the international border. Although Chiricahua is most closely aligned with the comparably high-elevation Huachuca, it also shares cold-tolerant subtropical taxa with clusters B and C.

The second biotic cluster (B) is defined by its center-located longitude while occurring at middle to lower latitudes within the region. An increase in longitude and latitude drives colder winter minimum temperatures, contributing to a distinct change in species composition. Although Peloncillo stretches considerably further north than other ranges in the second cluster, nearly all subtropical plant collections from Peloncillo are from the southern half of this sky island. Peloncillo represents the eastern boundary of significant regional subtropical influence (10.4% *PSR*), contrasted by substantial drops in the adjacent Animas (6.4% *PSR*) and Little Hatchet (3.6% *PSR*).

The third cluster (C) has the lowest level of within-cluster biotic similarity and occurs along the extreme eastern and northeastern fringe of the region. Here, subtropical influences diminish as community change occurs just east and north of this cluster along a regional ecotone. Cold Chihuahuan Desert temperatures manifest in the extreme eastern edge of the region in Animas and Little Hatchet, while the highest regional latitudes limit *PSR* in Pinaleño and Santa Teresa.

Galiuro is the only sky island that shares somewhat equal biotic similarity with clusters A and B. Several factors may contribute to this. The San Pedro River runs along its entire western perimeter and acts as a latitudinal corridor connecting sky islands in clusters A and B. Low-elevation Sonoran Desert habitat also occurs in the western foothills of Galiuro, sharing biotic

affinities with nearby sky islands aligned with cluster A (Rincon, Santa Catalina).

Three ranges (Big Hatchet, Little Dragoon, and Winchester) did not form significant relationships with the three subtropical clusters. Big Hatchet and Winchester may be explained by their depauperate representation in herbarium collections and minimal public access. When these two samples were removed from the analysis, annual precipitation was added as a driver of the longitudinal beta diversity gradient, which is supported by a generally decreasing volume of regional precipitation from west to east (McLaughlin 1995). Conversely, Little Dragoon is relatively well-collected and shares similarities with several nearby ranges (Dragoon, Whetstone), but is not statistically similar to any subtropical clusters.

Additionally, Galiuro, Little Dragoon, and Winchester appear to be on the geographical edge of two biotic regimes. To the southwest of these three ranges, dominant subtropical clusters and hotspots occur, while to the northeast, sky islands have relatively low subtropical richness. These three ranges are somewhat of a border area, which are not similar enough to be aligned with clusters on either side.

Climate change implications

Understanding the abiotic drivers of *PSR* in the sky islands provides insight into potential responses to anthropogenic global change. Although nighttime, summer, and winter temperatures have significantly risen in the Southwest over the past half-century, increases in winter temperatures are the most extreme (Ruddell et al. 2013, Vose et al. 2017, Gonzalez et al. 2018). As minimum winter temperatures substantially influence subtropical plant distribution, Osland et al. (2021) highlight the potential of some tropical species to expand their geographic range due to projections of global warming. However, the current 27-year megadrought in the Southwest is the worst since 800_{CE} (McClaran and Wei 2014, Williams et al. 2022), and models project a weakening of the North American Monsoon with high confidence (Pascale et al. 2019, Moon and Ha 2020, Wang et al. 2021). Regional winter precipitation has also decreased during the current multi-decade drought, while anomalies of winter rainfall shortages have increased in frequency and intensity (Bertelsen 2018, Verrier 2022).

While Osland et al. (2021) documented the northward expansion of six tropical plant taxa due to increasing winter temperatures, our analysis shows that 284 sky island subtropical plant species are jointly predicted by temperature and precipitation. These northern peripheral populations occupy specialized montane microhabitats, temporally buffering some taxa from prolonged environmental stress (Dobrowski 2011, McLaughlin et al. 2017). Mountain terrain receives increased precipitation due to atmospheric circulatory dynamics (Ruddiman 1997, Stewart et al. 2002, Antonelli et al. 2018) and offers substantially augmented water storage potential due to subsurface bedrock moisture and slope geodiversity (surface and subsurface rocks and fragments),

providing a vital resource during severe drought and reducing evapotranspiration (Dubinin et al. 2021, McCormick et al. 2021, Nardini et al. 2021). Conversely, the broad lowland and arid habitat separating the sky islands can act as a climate-driven dispersal barrier for some species due to significantly hotter temperatures, increased soil evapotranspiration, and reduced rainfall. Additionally, nearly half of sky island subtropical plants are rare or vulnerable species, which are not known to experience significant range expansion and perform poorly under diminished precipitation dynamics (Vincent et al. 2020). Hotter summer and winter temperatures precipitate vapor pressure deficits, promote soil evaporation, increase plant transpiration, reduce soil moisture, and intensify drought severity (Breshears et al. 2013). Long-term temperature increases have also caused substantial upward elevational range shifts (Breshears et al. 2008, Lenoir et al. 2008, Vitasse et al. 2021), which may be problematic in the sky islands where high elevation habitat is limited, and species can quickly exhaust vertical space (Urban 2018). When considering the precipitation needs of regional subtropical plant taxa, the factors discussed above present sizable challenges to northward range expansion during worsening drought conditions.

The increasing frequency and intensity of megafires cause stand-replacing burns resulting in dramatic community assemblage changes, including conversions from conifers to hardwoods and forests to shrub-dominated communities (Barton and Poulos 2018, Hagmann et al. 2021, O'Connor et al. 2021, Poulos et al. 2021). Recent severe fires in four Arizona sky islands have impacted more than half of their total area (Villarreal et al. 2019), while models project that Madrean sky islands will lose significant areas of montane habitat in the next few decades due to climate change (Yanahan and Moore 2019). While some peripheral populations are resilient (Channell and Lomolino 2000), rapid environmental change may precipitate local extinction events, altered community composition, and range contractions in edge species experiencing more extreme conditions than those at the core (Allen and Breshears 1998, Gibson et al. 2009). As seasonal precipitation is a strong driver of *PSR*, sky island subtropical plants are likely to be highly sensitive to weakened monsoon dynamics, especially when combined with increasing temperatures and intensified heat waves. Additionally, many regional subtropical taxa are habitat specialists at their northern periphery and may be vulnerable to accelerated rates of change.

Conservation significance

Identifying hotspots of subtropical species richness in the sky island region highlights important conservation considerations. Although biodiversity hotspots are typically defined by species richness, rarity (threat), or endemism, hotspots of species richness seldom coincide with rarity (Lombard 1995, Reid 1998) or endemism (Orme et al. 2005, Stohlgren et al. 2005). By contrast, rarity hotspots

are better predictors of biodiversity than those of species richness (Williams et al. 1996, Balletto et al. 2010). Spector (2002) proposed regional ecotones for conservation consideration due to their high beta diversity. Sky islands occurring within Santa Cruz County represent the greatest regional concentration of rare subtropical taxa. Encompassing just a tenth of the region, Atascosa, Patagonia, and the southern half of Santa Rita contain 77% of all rare subtropical taxa and 86% of regional subtropical plant species. A large aggregation of subtropical sky island taxa occurs within a regional ecotone, an area more likely to be sensitive to global change that could serve as an environmental indicator (Neilson 1991, Kitzberger 2012). Species occurring in ecotones and peripheral populations have been proposed for conservation consideration (Neilson 1993, Kitzberger 2012, Rehm et al. 2015), some of which may represent valuable genetic repositories due to phenotypic plasticity or potential adaptive genetic variation from environmental stress (Chevin and Hoffmann 2017, Hanson et al. 2017). Regional ecotones host a high density of peripheral species (Kark 2013) and also experience increased human disturbance (Soares-Filho et al. 2006, Kitzberger 2012, Körner 2012), highlighting an additional conservation concern. As many species may not adapt fast enough to rapid environmental change (Jump and Peñuelas 2005, Quintero and Wiens 2013, Radchuk et al. 2019), some peripheral populations may contribute vital genetic adaptations, supporting long-term species preservation (Gibson et al. 2009, Rehm et al. 2015, MacDonald et al. 2017).

Overall, sky island subtropical plants represent a valuable repository of rare species, as nearly half of all taxa are designated rare or vulnerable. Although plant species at the edge of their geographic range are more likely to be locally classified as rare, the primary subtropical hotspot (No. 1) within Santa Cruz County hosts an unusually large concentration of rare species. Rare species strongly contribute to functional diversity (Lyons et al. 2005, Leitão et al. 2016, Basile 2022) and anthropogenic land-use adversely alters functional diversity (Mayfield et al. 2010, Ribeiro et al. 2019, Matuoka et al. 2020), highlighting the potential conservation value of subtropical hotspots. An escalating feedback loop of climate change, habitat loss, invasive species, and human impacts punctuate the urgency of developing management approaches to preserve biological diversity. Our results suggest that identifying hotspots in regional ecotones may provide a useful method to discern areas of high conservation priority.

Conclusion

Sky island subtropical plant distribution is principally influenced by climate. Sky islands with the highest *PSR* are situated in the southwest corner of the region along the international border, while the primary subtropical hotspot lies mostly within Santa Cruz County. Our results identify three sky island clusters of subtropical similarity along a strong longitudinal trend from west to east. Additional drivers of beta

diversity include latitude and area. Nearly half of sky island subtropical plant species are rare or vulnerable, and the primary subtropical hotspot is a significant reservoir of rare species, which merits consideration in land-use management and planning.

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Author Contributions

James T. Verrier: Project administration, supervision, investigation, data curation, methodology, conceptualization, spatial analysis, validation, visualization, writing.

Kenneth Mulder: methodology, conceptualization, statistical analysis, validation, visualization, review/editing.

Data Accessibility Statement

All relevant data are within the Supplemental Material Section or publicly available through databases described in the Materials & Methods.

Supplemental Material

This material is available as part of the online article from <https://escholarship.org/uc/fb>

Fig. S1. Presence data for all subtropical plant taxa in the southwestern U.S. sky islands.

Fig. S2. Geographic extent, taxonomy, and lifeform type for all southwestern U.S. sky island subtropical plant taxa.

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