

Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island ecosystem, Arizona, USA

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Abstract The Sky Island archipelagos of the Sierra Madre Occidental contain diverse, highly endemic, and topographically complex ecosystems, yet the local and landscape-scale controls on woody plant dominance and diversity patterns are poorly understood. This study examines variation in woody plant species composition in relation to a suite of environmental variables (i.e., elevation, potential soil moisture, soil type, geologic substrate, and heat load) in the Chiricahua National Monument, Arizona (CHIR). Nine vegetation types were identified using cluster analysis that varied by species composition and plant life form. Non-metric multidimensional scaling and correlation analyses identified significant relationships between vegetation composi-

tion and elevation, potential soil moisture, and heat load. Rarefied species richness varied among vegetation types, and in relation to topography, with higher species richness occurring on more topographically complex sites. β (species turnover) and γ (landscape) diversity were also high in CHIR compared to other temperate forests. This study highlights the importance of local- and landscape-scale environmental controls on species diversity and vegetation patterns in Madrean evergreen woodlands.

Keywords Species diversity · Cluster analysis · Ordination · Gradient analysis · Madrean evergreen woodlands · Sky Islands

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Introduction

The Sky Island forests of the Sierra Madre Occidental comprise one of the most diverse temperate forest ecosystems in the world (Whittaker and Niering 1975; Peet 1978; Whittaker et al. 1979; Felger and Wilson 1994; Warshall 1994). The primary reason for the high diversity of these forests is the mixing of Neotropical and Holarctic floras and the overlap of subtropical and temperate climatic zones in complex mountainous terrain (Coblentz and Riitters 2004). Elevation and topography play key roles in determining plant distribution and biodiversity

patterns in the Southwest (Whittaker and Niering 1975; Peet 1978; Whittaker et al. 1979; Wentworth 1981; Allen and Peet 1990; Barton 1994; Brown 1995; Parker 1995, 1996). Yet, variation in species distribution, plant diversity, and species packing of vegetation in relation to topography has only been examined in three sites in Arizona (Whittaker and Niering 1965, 1968, 1975; Wentworth 1981; Niering and Lowe 1984; Huebner and Vankat 2003).

Geographic variation in topography, solar radiation, geology, and soils contribute strongly to landscape- and regional-scale differences in woody plant distribution and diversity patterns including species richness (α -diversity) and species turnover (β -diversity) (Christensen and Peet 1984; Allen et al. 1991; Urban et al. 2000). Topography facilitates the compression of biotic communities into relatively constricted vertical spaces (McLaughlin 1994), where areas of higher topographic complexity support higher species richness (Felger and Wilson 1994). Limited data suggest that species turnover (β -diversity) in Sky Islands is high relative to other forest types in western North America (Whittaker and Niering 1965; Peet 1978), though data only exist for the Santa Catalina Mountains in the Sierra Madre Occidental.

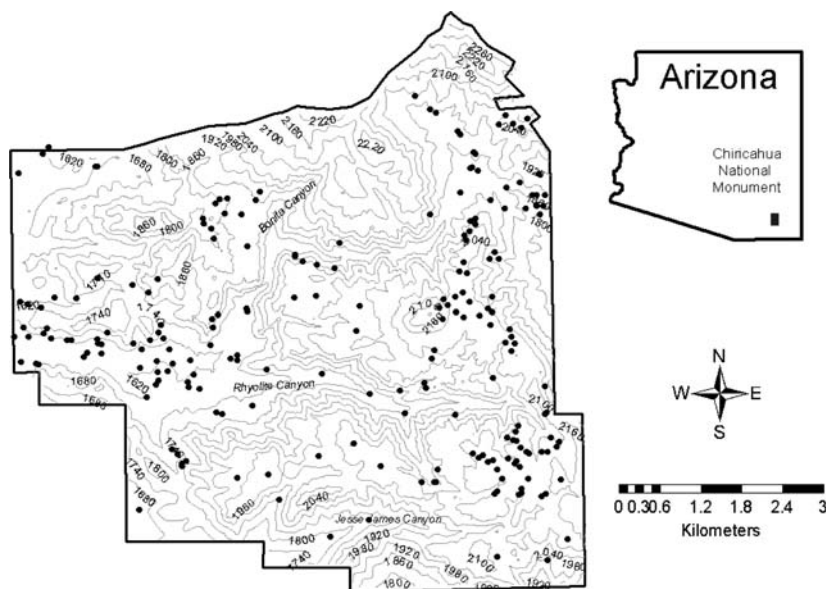
The study builds on the limited knowledge of the relationship between the dominance and

diversity of woody plant species and environmental variation in the American Southwest. Our specific objectives were to: (1) Identify the patterns of woody plant distributions and abundance across a complex topographic gradient, (2) Relate the variation in woody species distribution and abundance patterns to spatial environmental variation, (3) Identify the relationships among plant diversity, life-form, and environmental variation, and compare species diversity among vegetation types, and (4) Quantify variation in the structural and growth form diversity among different vegetation types and relate these differences to environmental gradients.

Study area

Madrean vegetation was studied in the Chiricahua National Monument in southeastern Arizona (CHIR) (Fig. 1) in the northern edge of the Sierra Madre Occidental, a major mountain range that extends 1,500 km from southeast Arizona through Sonora and Chihuahua to the Rio de Santiago in Jalisco, Mexico. Soils in CHIR are shallow and are derived from volcanic rhyolites and monzonites deposited in the early- to mid-Miocene, though pre-Tertiary rock is prominent at lower elevations (Drewes and Williams 1973).

Fig. 1 Map of the Chiricahua National Monument, Cochise County, Arizona. Sampling points ($n = 200$) are indicated with a dot



Elevations range from 1,566 m to 2,372 m. The terrain is rugged and extremely complex, consisting of incised towers and rocky uplands separated by steep walled canyons that drain into Sulfur Springs Valley.

The climate in CHIR is arid to semiarid, and is characterized by cool, wet winters and hot summers. Mean monthly minimum and maximum temperatures range from -0.2°C to 14.7°C in January to 17.4°C and 32.8°C in July (Sellers et al. 1985). Precipitation is bimodal, with wet winters, a pronounced dry spring and early summer, wet mid and late summer, and a fall drought. Mean annual rainfall at 1,650 m at the Southwestern Research Station in the Coronado National Forest adjacent to CHIR is 506 mm.

Evergreen forests dominate high elevations in CHIR. These forests are a mixture of both needle-leaf (e.g. *Pinus* sp.) and broadleaf (e.g. *Quercus* sp.) evergreen species. Woodlands are dominated mainly by tree life forms of oak (*Quercus emoryi*, *Q. hypoleucoides*, *Q. toumeyii*, *Q. rugosa*, and *Q. arizonica*), juniper (*Juniperus deppeana* and *J. monosperma*), and pine (*Pinus discolor*, *P. edulis*, *P. leiophylla*, *P. engelmannii*, and *P. ponderosa*). Semi-desert grasslands mixed with shrubs and cacti including *Cercocarpus montanus*, *Garrya wrightii*, *Yucca schottii*, *Nolina microcarpa*, *Opuntia engelmannii*, *O. spinosior* occupy low elevations. Interior Petran chaparral dominates dry sites at middle and upper elevations. Prominent chaparral species include: *Arctostaphylos pungens*, *C. montanus*, and *G. wrightii*, which are often intermixed with shrub oaks (i.e., *Q. emoryi*, *Q. hypoleucoides*, *Q. toumeyii*, *Q. rugosa*, *Q. turbinella*, and *Q. arizonica*). Pine-oak woodlands are dominated by pinyon, juniper, and oak trees with an open understory of shrubs. Gallery forests occupy mesic canyons where evergreen conifers (*P. leiophylla*, *P. discolor*, *P. engelmannii*, *P. ponderosa*, *Cupressus arizonica*, and *Pseudotsuga menziesii*) form an emergent canopy layer above understory oaks (*Q. emoryi*, *Q. hypoleucoides* and *Q. arizonica*). Nomenclature follows Bailey and Hawksworth (1983) for Pinaceae and Kearney and Peebles (1960), as updated by Lehr (1978), for all other species.

Field methods

Data collection

Sample sites were distributed among vegetation cover types identified by Kluber (2000) from aerial photographs that were classified based on the cover of different plant life-forms (i.e., tree, shrub, and grass) as follows:

1. Grassland: high grass cover, tree and shrub cover <10%
2. Savanna: high grass cover, tree and shrub cover 10–25% cover
3. Open woodland: tree canopy patchy, grass in the understory; tree cover 25–60%
4. Closed woodland: tree canopy continuous, often overlapping, tree cover >60% cover
5. Open chaparral: shrub canopy patchy, shrub cover 25–60%
6. Closed chaparral: shrub canopy continuous, often overlapping, shrub cover >60%

We selected 200 points to sample vegetation in the field from the map produced by Kluber (2000). The number of points in each cover type was proportioned to the area of each cover type on the map. Sample points were placed in the center point of homogeneous cover type areas larger than 1,800 m² on Kluber's (2000) vegetation map due to the fact that random, or systematic sampling was impossible in such a dissected landscape. The extremely complex terrain with vertical rhyolitic towers limited our sampling to slopes <30° that were accessible by foot.

Vegetation at each point was sampled using a belt transect of 5–20, 5 × 5 m quadrants. Transect length varied depending on vegetation density, and was established parallel to the slope contour. At each point the location (GPS), elevation, slope aspect and pitch, topographic position, slope configuration, soil type, and geologic substrate (Denny and Peacock 2000) were recorded. In each quadrant, we measured the basal diameter of all shrubs and trees >10 cm of each genet, counted seedlings, shrubs and cacti (stems <10 cm basal diameter), and estimated percent cover for each woody species in one of six cover classes (<1, 1–4, 5–24, 25–49, 50–74, and 75–100%).

Data analyses

Groups of plots with similar woody plant composition were identified using cluster analysis. First, we calculated an importance value (range 0–200) for each species in each plot as the sum of relative frequency (presence and absence in 5 m blocks) and relative cover. Second, we clustered species' importance values using Ward's method, and relative Euclidean distance as the similarity measure with PC-Ord software (McCune and Mefford 1999). Ward's method minimizes the within-group variance relative to among-group variance (Tabachnick and Fidell 2001). We then identified differences between species importance values and environment (i.e., elevation, heat load, aspect, and topographic relative moisture index) among groups by comparing mean values of environmental variables for each group using a distribution-free Kruskal–Wallis H test. The topographic relative moisture index (TRMI) (Parker 1982) is a topographically based measure of relative site moisture availability based on topographic features (slope aspect and pitch, slope position, slope configuration) that ranges from 0 (xeric) to 60 (mesic). Direct incident solar radiation or heat load was calculated following McCune and Keon (2002).

Variation in species composition among sites was analyzed using non-metric multidimensional scaling (NMDS) (Kruskal and Wish 1978) and PC-Ord software (McCune and Mefford 1999), and the potential contribution of environmental variables in explaining variation in species abundance was identified by correlating (Pearson product moment) NMDS axis scores with elevation, TRMI, and heat load. NMDS differs fundamentally from other ordination methods in its reliance on a dissimilarity matrix for the calculation of distances, rather than a chi-square metric, and it generally outperforms other ordination methods due to its non-metric nature (Prentice 1980; Gauch et al. 1981; Kenkel and Orlóci 1986; Minchin 1987). NMDS is an iterative search for a ranking and placement of n entities on k dimensions (axes) that minimizes the stress of the k -dimensional configuration (McCune and Grace 2004). The calculations are based on an $n \times n$ distance matrix calculated from the $n \times p$ -dimen-

sional main matrix, where n is the number of rows and p is the number of columns in the main matrix. “Stress” is a measure of departure from monotonicity in the relationship between the dissimilarity (distance) in the original p -dimensional space and distance in the reduced k -dimensional ordination space.

Diversity estimates

We assessed variation in species diversity at three scales: within vegetation types (α), among vegetation types (β), and across the landscape (γ). Species' counts in 5×25 m plots were used for all diversity calculations to standardize for differences in transect length (Whittaker 1972; Melo et al. 2003). Species richness (S_{obs}), Simpson diversity (τ), Shannon diversity (H'), were used as measures of alpha diversity (α), along with two non-parametric incidence-based species richness estimators, Chao₂ and Jack₂ (e.g. Whittaker 1972; Magurran 2004). Chao₂ and Jack₂ are robust sample-based species richness estimators that estimate species richness in a species pool using maximum likelihood methods (Chazdon et al. 1998). Chao₂ is a richness estimator that emphasizes the importance of species that occur only as singletons and doubletons in species richness estimation, while Jack₂ is a second order jackknife estimator of species richness (Magurran 2004). Formulas and descriptions of their performance can be found in Chazdon et al. (1998) and Chao (1987). We constructed sample-based rarefaction curves (species accumulation as a function of occurrence) with 95% confidence intervals (Colwell et al. 2004) to assess sampling completeness and to compare differences in species richness among vegetation types using *EstimateS* software (Version 7.5, Colwell 2005). Rarefaction differs from classical species area curves (e.g. MacArthur and Wilson 1967), which plot the cumulative number of species recorded (S) as a function of sampling effort (n). Instead, rarefaction plots the total number of individuals counted with repeated random sampling against the total number of species found in those samplings (Colwell and Coddington 1994). Sample-based rarefaction permits comparison of species richness (S_{obs}) among groups with different sample

sizes using a Monte Carlo randomization procedure (Gotelli and Colwell 2001). Chao_2 and Jack_2 were also computed as a function of the sample accumulation level (Chazdon et al. 1998) to reduce the bias that under sampling may impose on total species richness estimates.

Variation in Beta (β) diversity, or the degree to which different vegetation types share species, was identified using Jaccard and Sørensen similarity indices modified and scaled by Chao et al. (2005) to accommodate for sample size differences.

Gamma (γ), or landscape diversity was estimated using all of the plots to identify species richness at the landscape scale. Gamma diversity was calculated by constructing a rarefaction curve for all samples and all species in the CHIR landscape.

Structural diversity was assessed through rarefaction using the density (ha^{-1}) of trees (saplings <10 cm basal diameter and trees \geq 10 cm basal diameter) in 5 cm size-classes by species for each vegetation type. H' and τ diversity were also calculated for each vegetation type using size-class data as a measure of α -diversity.

Results

Vegetation types

Nine vegetation types were identified from the cluster analysis of species importance values (Table 1, Fig. 2). Vegetation types differed by species composition, elevation, soil moisture (TRMI), soil type, geologic substrate, and heat load ($P < 0.01$ Kruskal–Wallis test). A three dimensional solution was obtained by the NMDS of species importance values, which separated samples by species composition, elevation, TRMI, and heat load (Fig. 2, Table 2). The first NMDS axis separated samples according to elevation, TRMI and heat load. Elevation and TRMI were negatively correlated to axis 1, while heat load was positively correlated, indicating that increases in altitude and soil moisture resulted in reduced heat loads. A negative correlation between NMDS axis 2 and elevation, and a positive correlation with TRMI showed further sorting between vegetation and low-elevation, wet and high-elevation, dry sites. Species richness, H' , and

τ diversity were positively correlated with NMDS axis 1, and negatively correlated to axis 2.

The three gallery forest types (lowland, mid-elevation, and upland) were characterized by high basal area of mesophytic tree species, which were found in mesic drainages with heavy accumulations of alluvial riverwash (Table 1, Figs. 2, 3). Lowland, mid-elevation, and upland gallery forest were differentiated by turnover in species composition with increasing elevation (Tables 1, 2). Pinyon pine-white oak forest occurred at mid to high elevations (1,840–2,040 m) on drier sites on soils of the Whitebuck–Huachuca–Yaquican complex derived from volcanic lava flows and sedimentary rocks rich in volcanic debris. Soils in this vegetation type were composed of cobly loam covered with leaf litter. Manzanita-juniper-white oak stands occurred at middle elevations (1,590–1,985 m) of intermediate soil moisture on unconsolidated or poorly consolidated silt, sand, and gravel soils of mid-elevation side slopes. Juniper-oak forests occurred on low to mid-elevation (1,585–1,985 m) side slopes of intermediate potential soil moisture on the same soils and substrates as manzanita-juniper-white oak forests. The manzanita-oak scrub vegetation type was the dominant high elevation (1,940–2,160 m) chaparral vegetation type on south-facing, xeric sites. This chaparral vegetation type was found on moist hailstone soils that are loamy-skeletal and underlain by rhyolitic tuff bedrock. The oak-pinyon pine-manzanita vegetation type was the other important chaparral type on xeric sites that occurred over a range of elevations (1,660–2,160 m). This vegetation type was found on Atascosa-Canpicket soils derived from rhyolitic tuff outflow faces, which were poor soils composed of rock outcrops and areas of exposed bedrock. Mountain mahogany (*Cercocarpus montanus*) scrub was restricted to low elevation (1,655–1,860 m), xeric sites on lava flow derived substrates with low basal area.

Species diversity

Alpha diversity

Species richness varied by vegetation type in CHIR (Fig. 4). The majority of sample-based species

Table 1 Mean, minimum, and maximum elevation, relative soil moisture (TRMI), and heat load for vegetation types identified by cluster analysis of species IV in Chiricahua National Monument, Arizona. Dominant soil types (>75% of plots) for each compositional group are also listed

Vegetation type	Dominant species	Geologic substrate	Elevation (m)	TRMI	Heat load
Mountain mahogany ($n = 10$)	<i>Cercocarpus montanus</i>	Atascosa-Canpicket tuff outflow	1,734	30	0.92
	<i>Nolina microcarpa</i>		1,655	17	0.56
	<i>Garrya wrightii</i>		1,860	43	1.12
Oak-Pinyon-Manzanita ($n = 54$)	<i>Quercus toumeyii</i>	Atascosa-Canpicket tuff outflow/Hailstone	1,930	26	0.93
	<i>Pinus discolor</i>		1,660	10	0.54
	<i>Arctostaphylos pungens</i>		2,160	48	1.13
Manzanita-oak ($n = 41$)	<i>A. pungens</i>	Moist Hailstone	2,100	26	0.90
	<i>Q. hypoleucoides</i>		1,940	10	0.62
	<i>Q. toumeyii</i>		2,160	54	1.08
Juniper-oak ($n = 25$)	<i>P. discolor</i>	Atascosa-Canpicket tuff outflow	1,725	39	0.87
	<i>Juniperus deppeana</i>		1,585	8	0.77
	<i>Q. arizonica</i>		1,985	59	0.91
Manzanita-juniper-white oak ($n = 26$)	<i>A. pungens</i>	Atascosa-Canpicket tuff outflow	1,724	38	0.92
	<i>J. deppeana</i>		1,623	23	0.74
	<i>Q. arizonica</i>		1,920	54	1.07
Pinyon-white oak ($n = 10$)	<i>P. edulis</i>	Whitebuck-huachuca-yaquican complex	1,946	27	0.98
	<i>Q. arizonica</i>		1,840	14	0.76
	<i>J. deppeana</i>		2,040	43	1.09
Lowland gallery forest ($n = 11$)	<i>Cupressus arizonica</i>	Otroizo-riverwash complex	1,750	42	0.91
	<i>J. deppeana</i>		1,615	30	0.87
	<i>Q. arizonica</i>		1,990	59	0.97
Mid-elevation gallery forest ($n = 11$)	<i>Platanus wrightii</i>	Otroizo-riverwash complex	1,851	44	0.81
	<i>Q. hypoleucoides</i>		1,665	19	0.59
	<i>P. engelmannii</i>		2,025	58	1.00
Upland gallery forest ($n = 12$)	<i>P. leiophylla</i>	Otroizo-riverwash/moist hailstone	2,112	34	0.84
	<i>P. ponderosa</i>		1,975	18	0.57
	<i>Q. hypoleucoides</i>		2,170	46	1.02
	<i>Pseudotsuga menziesii</i>				

Elevation, relative soil moisture, and heat load varied among vegetation groups ($P < 0.001$ Kruskal–Wallace). TRMI varies between 0 (Xeric) and 60 (mesic), and heat load varies between 0.5 and 1.5

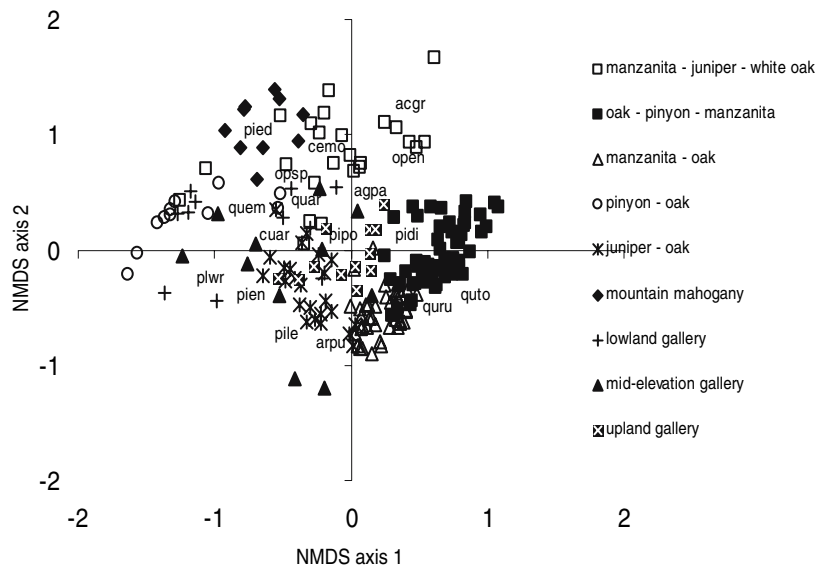


Fig. 2 Non-metric multidimensional scaling of samples ($n = 200$) based on species importance values. Different symbols represent species composition groups identified by cluster analysis (Table 1). Abbreviations: acgr = *Acacia greggii*, agpa = *Agave palmeri*, arpu = *Arctostaphylos pungens*, cemo = *Cercocarpus montanus*, cuar = *cupressus*

arizonica, open = *Opuntia engelmannii*, opsp = *Opuntia spinosior*, pidi = *Pinus discolor*, pied = *Pinus edulis*, pien = *P. engelmannii*, pile = *P. leophylla*, pipo = *P. ponderosa*, plwr = *Platanus wrightii*, quar = *Quercus arizonica*, quem = *Q. emoryi*, quru = *Q. rugosa*, and quto = *Q. toumeyi*

accumulation curves for each vegetation type reached an asymptote except for mid-elevation gallery forests, indicating that sampling was insufficient for species richness estimation of this vegetation type. The Jack₂ and Chao₂ estimators also indicated that sampling efficiency was high (Table 3). As expected, Jack₂ and Chao₂ estimated greater minimum species richness than the observed values for each vegetation type (Table 3). For example, we counted 21 species in the mid-elevation gallery vegetation type, though Chao₂ estimated a minimum species richness of 37.

Alpha diversity (S_{obs} , H' , τ) was highest in low elevation juniper-oak forest, and lowest in upland gallery forest (Table 3, Fig. 4). Vegetation types with high α -diversity, also had higher numbers of singletons (Table 3). Juniper-oak forests had significantly higher species richness than other vegetation types when rarefaction curves were plotted within 95% confidence intervals, upland gallery forest species richness was significantly lower than lowland and upland gallery forest, oak-pinyon-manzanita, and manzanita-juniper-white oak vegetation types (Fig. 5). Juniper-oak

forests also had a higher projected asymptote than other vegetation types.

Beta diversity

The Sorenson and Jaccard similarity measures indicated high β -diversity between vegetation types (Table 4), and the rarefaction curves indicate a greater rate of change in species richness in the juniper-oak vegetation type than the other groups (Fig. 4). Lowland vegetation types were floristically dissimilar from upland communities, while mid-elevation vegetation types shared species from lowland and upland vegetation types. Similarly, there was overlap in the species composition of vegetation types according to similarities in elevational distribution, heat load, soil type, and geologic substrate. Low elevation types including mountain mahogany, lowland gallery, and juniper-oak shared many species. Upland vegetation types including upland gallery forest and manzanita-oak also shared species. Pinyon-white oak and mid-elevation gallery forest types had high species overlap, while mid-elevation

Table 2 Pearson product moment coefficients ($n = 200$) of species importance values, environmental variables, and species diversity for NMDS axes 1, 2, and 3 from plots in Chiricahua National Monument, Arizona

Species	Axis 1	Axis 2	Axis 3
<i>Acacia gregii</i>	0.192	0.076	-0.131
<i>Agave palmerii</i>	0.241	0.05	-0.335
<i>Arctostaphylos pungens</i>	0.319	-0.227	0.792
<i>Cercocarpus montanus</i>	0.171	0.019	-0.467
<i>Cupressus arizonica</i>	-0.327	0.176	0.028
<i>Dasyllirion wheeleri</i>	0.484	-0.126	-0.114
<i>Ericameria laricifolia</i>	0.297	0.053	-0.227
<i>Garrya wrightii</i>	0.179	-0.326	-0.324
<i>Juniperus deppeana</i>	0.061	0.664	-0.188
<i>Nolina microcarpa</i>	0.146	-0.089	-0.381
<i>Opuntia engelmannii</i>	0.178	-0.038	-0.283
<i>Opuntia spinosior</i>	0.092	0.106	-0.163
<i>Pinus discolor</i>	0.034	-0.593	0.068
<i>Pinus edulis</i>	-0.045	0.235	-0.45
<i>Pinus engelmannii</i>	-0.25	0.207	-0.006
<i>Pinus leiophylla</i>	-0.255	0.122	0.261
<i>Pinus ponderosa</i>	-0.619	0.016	-0.01
<i>Platanus wrightii</i>	-0.116	0.254	0.031
<i>Pseudotsuga menziesii</i>	-0.491	-0.021	0.008
<i>Quercus arizonica</i>	-0.183	0.329	-0.482
<i>Quercus emoryi</i>	0.15	0.405	-0.167
<i>Quercus hypoleucoides</i>	-0.664	-0.041	0.234
<i>Quercus rugosa</i>	-0.29	-0.214	0.094
<i>Quercus toumeyii</i>	0.377	-0.724	0.187
<i>Rhus choriophylla</i>	0.185	-0.212	-0.054
<i>Rhus trilobata</i>	0.007	0.135	-0.058
<i>Yucca baccata</i>	0.027	-0.221	0.033
<i>Yucca schottii</i>	0.009	0.227	-0.391
Heat load	0.255	-0.059	-0.028
Elevation	-0.395	-0.457	0.316
TRMI	-0.138	0.512	-0.081
Species richness	0.155	-0.090	-0.310
Shannon	0.218	-0.171	-0.162
Simpson	0.199	-0.231	-0.066

Values greater than 0.138 are significant to $P < 0.05$, and values greater than 0.181 are significant to $P < 0.01$

gallery forest and chaparral vegetation types had intermediate species overlap.

Gamma diversity

Landscape, or γ -diversity, reached an asymptote at approximately 100, indicating that the study area was sufficiently sampled (Fig. 6). Total, rarefied species richness for the study area was 47.

Structural diversity

Lowland and mid-elevation gallery forests were the most structurally diverse vegetation types in CHIR (Fig. 7). They occupied mesic sites and

alluvial soils, while less vertically and horizontally diverse vegetation types dominated hot, xeric sites on shallow, nutrient poor soils on side slopes. Lowland gallery forest was the most structurally diverse vegetation type based on rarefaction curves plotted within 95% confidence intervals, and all other vegetation types were significantly less structurally diverse. Lowland gallery forest also had the highest rate of increase and the highest projected structural complexity for any vegetation type (Fig. 7). Mid-elevation gallery forest was the next most complex, followed by other tree-dominated vegetation types: juniper-oak, manzanita-juniper-white oak, pinyon-white oak, and upland gallery forest. Chaparral

Fig. 3 Species basal area (m^2/ha) by vegetation type (Table 1) in Chiricahua National Monument, Arizona. Vegetation types were identified by cluster analysis using relative Euclidean distances and Ward's method

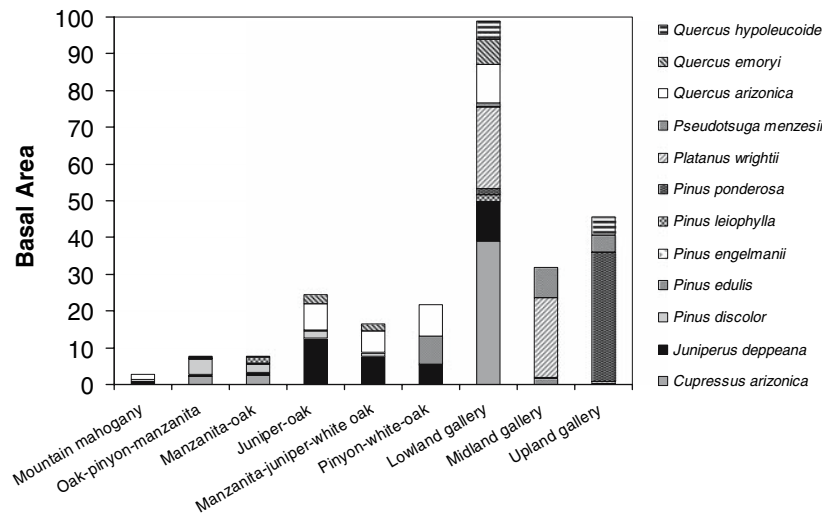
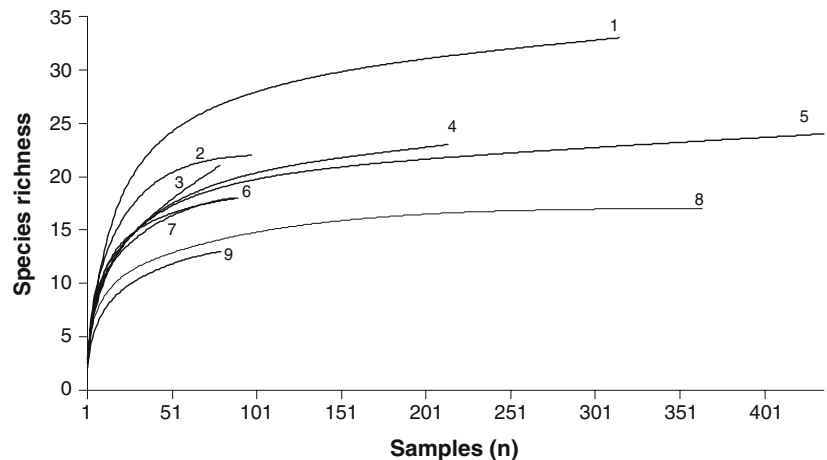


Fig. 4 Sample-based rarefaction curves of plots in each vegetation type, Chiricahua National Monument, Arizona. Numbers correspond to vegetation types as follows: 1 = juniper-oak, 2 = lowland gallery, 3 = mid-elevation gallery, 4 = manzanita-juniper-white oak, 5 = oak-pinyon-manzanita, 6 = pinyon-white oak, 7 = mountain mahogany, 8 = manzanita-oak, and 9 = upland gallery



vegetation types (manzanita-oak, oak-pinyon-manzanita, and mountain mahogany), which occur on dry sites with poor soils, were the least structurally complex because they were dominated by dwarf shrubs and trees with a similar life form.

Discussion

Species–environment relationships

Elevation and soil moisture were the dominant controls on species diversity and plant species composition and abundance in CHIR. While elevation was the major influence on species'

distributions, soil moisture, heat load, soil type, and geologic substrate further contributed to species' segregation. For example, the species composition of the three different gallery forest types varied with elevation, but all gallery forest types occurred on mesic sites on deep soils derived from riverwash alluvium. In contrast, juniper-oak forests spanned a similar elevation range as lowland gallery forests, but they occupied drier, hotter sites with shallow soils derived from tuff outflow.

The species–environment relationships in CHIR are similar to those reported for other Arizona mountain ranges including the Santa Catalina Mountains (Whittaker and Niering 1965, 1968, 1975), the Mule Mountains (Wentworth

Table 3 Jack₂ and Chao₂ species richness, singletons, doubletons, sampling efficiency, and Harrison's β -diversity estimates for woody plant diversity for each vegetation type in Chiricahua National Monument and the percentage of the expected collected

Vegetation type	Species observed	Jack ₂ % Collected	Chao ₂ % Collected	Singletons	Doubletons	Shannon Diversity	Simpson Diversity	Beta Diversity
Juniper-oak	33	43	46	2	3	1.45 ± 0.58	0.65 ± 0.24	9.38
Upland gallery	13	14	14	0	1	1.00 ± 0.29	0.53 ± 0.14	23.44
Pinyon-white oak	18	18	19	2	4	1.85 ± 0.22	0.8 ± 0.04	14.06
Midland gallery	21	35	60	2	0	1.65 ± 0.33	0.74 ± 0.10	21.88
Manzanita-oak	17	16	17	8	2	1.58 ± 0.27	0.75 ± 0.07	35.94
Manzanita-juniper-white oak	23	31	31	1	2	1.80 ± 0.30	0.79 ± 0.07	19.19
Mountain mahogany	18	20	19	4	0	1.78 ± 0.30	0.78 ± 0.07	15.63
Lowland gallery	22	23	22	4	0	1.50 ± 0.37	0.7 ± 0.14	7.91
Oak-pinyon-manzanita	24	32	32	5	0	1.62 ± 0.26	0.74 ± 0.07	15.63

1981), the Prescott National Forest in northern Arizona (White and Vankat 1993; Huebner and Vankat 2003), and Cave Creek Canyon (Barton 1994), just outside CHIR. These studies also identified elevation, soil moisture, and substrate type as important variables that contribute to species' sorting patterns. Furthermore, Barton (1994) identified the same environmental variables as we did in this study (elevation, soil moisture, and substrate type) as important controls on woody plant distributions in a less topographically dissected and geologically different portion of the same mountain range as CHIR.

Sorting of species by elevation and potential soil moisture in CHIR and other Southwestern mountains is, in part, explained by variation in species' tolerance to drought (Stephenson 1990, 1998; O'Brien et al. 2000). For example, junipers (Padien and Lajtha 1992) tolerate lower pre-dawn and mid-day water potentials than pinyon pine (Linton et al. 1998). They are also more resistant to xylem cavitation (Linton et al. 1998), suggesting they can tolerate lower soil moisture levels than pinyon pine without disruption of water conduction or transport. The dominance of alligator juniper on low elevation xeric sites compared to dominance of pinyons at mid to high elevations in CHIR and other Sky Island ecosystems is consistent with their physiological capacity to tolerate drought (Niering and Lowe 1984; Martens et al. 2001).

Although pinyon pines are less drought tolerant than junipers, they are more drought tolerant than other pines in the Southwest. Field and greenhouse drought experiments on pines of the Chiricahua Mountains indicated that pinyon pines survived longer than other pines under persistent drought conditions and they experienced little change in internal water potential, while other species of pines experienced a precipitous decline in water potential that was ordered by their elevational distribution (*P. discolor* > *P. leiophylla* > *P. ponderosa*) (Barton 1993; Barton and Teeri 1993). Moreover, pinyon pine also experienced less depression of photosynthesis relative to other species, suggesting that it was more tolerant of drought conditions than the other pines in this study. Field experiments of seedling survival under varying light, litter, and moisture

Fig. 5 Rarefied species number and upper 95% confidence interval for vegetation types (Table 1) identified by cluster analysis of species importance values for Chiricahua National Monument, Arizona

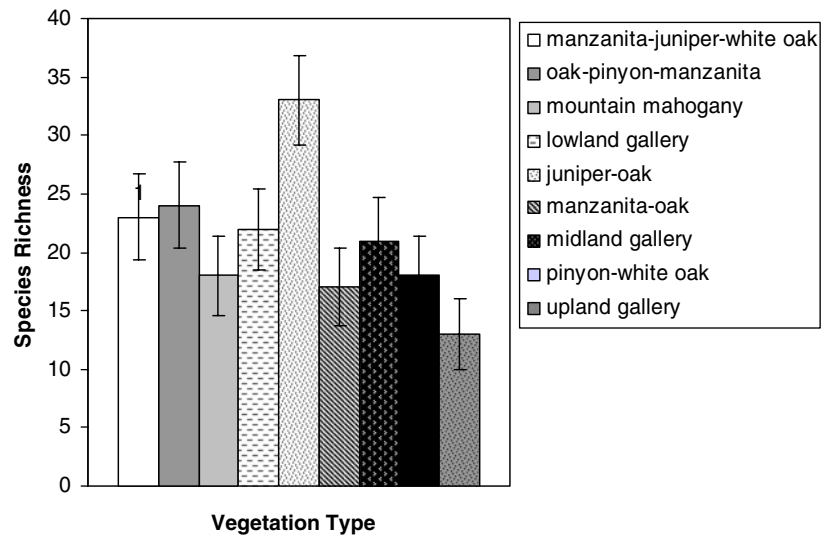
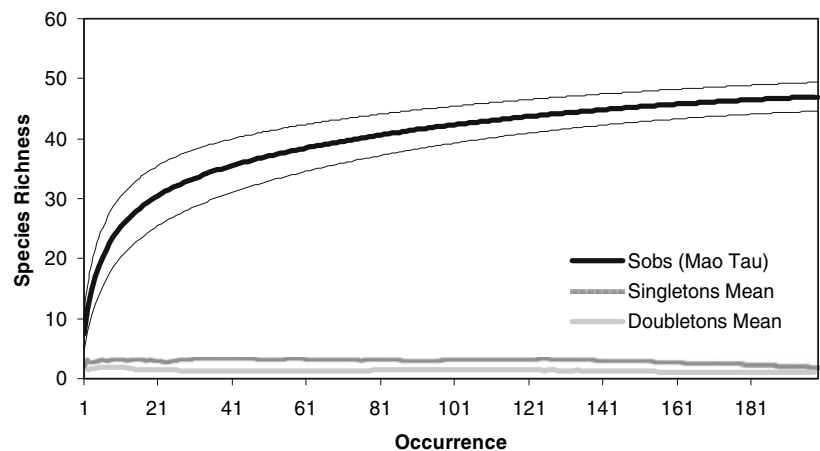


Fig. 6 Gamma diversity estimates for Chiricahua National Monument using sample-based rarefaction curves and 95% confidence intervals for all woody plant species ($n = 47$) based on 200 vegetation samples)



conditions (Barton 1993) corroborate findings from Barton and Teeri's (1993) greenhouse drought experiments, further demonstrating that plant water stress tolerance is a dominant control on the elevational distribution of pines in the Chiricahua Mountains.

The distribution of other woody plant species in CHIR was also probably related to individual species' adaptations to water availability. Manzanita (i.e., Davis and Mooney 1986), scrub oaks (i.e., Hamerlynck and Knapp 1994; Keeley 1998), and other chaparral species (i.e., Davis et al. 1999; Balok and St. Hilaire 2002) are generally found on harsh sites (i.e., low soil moisture, poor soils, etc.), and are known to be extremely tolerant of drought by maintaining extremely negative water

potentials under dry conditions. Moreover, many chaparral species are extremely deep rooted, which gives them access to moisture low in the water table (Davis and Mooney 1986). This pattern was the same in CHIR, where drought tolerant chaparral vegetation types dominate the most xeric sites.

Alpha diversity patterns

Species richness was highest for juniper-oak, oak-pinyon-manzanita, and low and mid-elevation gallery forest vegetation types that had wide elevational distributions. The wide elevation ranges of these vegetation types corresponded to high topographic variability across the

Table 4 Chao–Jaccard and Chao–Sorensen similarity in woody plant species composition between vegetation types in Chiricahua National Monument

	Mountain Mahogany	Oak–pinyon–manzanita	Manzanita–oak	Juniper–oak	Manzanita–Juniper–white oak	Pinyon–white oak	Lowland gallery	Middle elevation gallery	Upland gallery
Chao–Jaccard									
Mountain Mahogany	X								
Oak–pinyon–manzanita	0.84	X							
Manzanita–oak	0.53	0.96	X						
Juniper–oak	0.7	0.53	0.43	X					
Manzanita–Juniper–white oak	0.34	0.55	0.56	0.49	X				
Pinyon–white oak	0.77	0.64	0.59	0.61	0.62	X			
Lowland gallery	0.96	0.76	0.71	0.97	0.82	0.88	X		
Middle elevation gallery	0.41	0.75	0.72	0.67	0.59	1	0.79	X	
Upland gallery	0.13	0.71	0.89	0.33	0.7	0.42	0.42	0.56	X
Chao–Sorensen									
Mountain Mahogany oak pinyon	X								
Manzanita	0.91	X							
Manzanita–oak	0.69	0.98	X						
Juniper–oak	0.82	0.69	0.61	X					
Manzanita–juniper–white oak	0.51	0.71	0.72	0.65	X				
Pinyon–white–oak	0.87	0.78	0.74	0.76	0.76	X			
Lowland gallery	0.98	0.86	0.83	0.98	0.9	0.93	X		
Middle elevation gallery	0.58	0.86	0.83	0.8	0.74	1	0.88	X	
Upland gallery	0.23	0.83	0.94	0.5	0.82	0.59	0.59	0.72	X

elevational gradient of CHIR. Uplands have highly dissected topography consisting in mountain plateaus intermixed with towers of rhyolitic tuff, while lowlands are flatter, with lower variation in topographic complexity. Vegetation types that span a range of elevations are therefore exposed to a mixture of topographic conditions or potential habitats for plant colonization, and this may explain the higher species richness of widely distributed vegetation types in CHIR.

These patterns correspond to Whittaker and Niering's (1965, 1968, 1975) work in the Santa Catalina Mountains who also found high α -diversity in open oak and pygmy conifer woodlands that existed on similar sites to juniper–oak wood-

land sites in CHIR, suggesting that this trend may occur in other Sky Island Mountains as well. Woody species richness is higher in CHIR than the Santa Catalina Mountains (Whittaker and Niering 1965), which could be attributed to the greater topographic complexity of CHIR relative to the Santa Catalinas. In general, species richness has been attributed to high topographic complexity in Sky Island Mountains (Coblentz and Riitters 2004, 2005). The terrain in CHIR is highly dissected and erosion of the rhyolitic tuff creates incised towers and steep slopes that promote vertical stacking of biotic communities, amplifying the array of potential sites for plant establishment and growth compared to terrain in

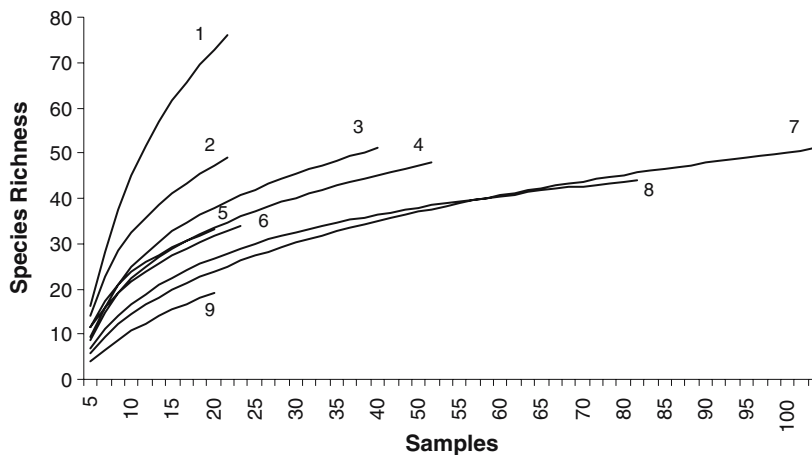


Fig. 7 Sample-based rarefaction curve for richness of woody plant size structure for each vegetation type in Chiricahua National Monument, Arizona. Numbers correspond to vegetation types as follows: 1 = lowland

gallery, 2 = mid-elevation gallery, 3 = juniper-oak, 4 = manzanita-juniper-white oak, 5 = pinyon-white oak, 6 = upland gallery, 7 = oak-pinyon-manzanita, 8 = manzanita-oak and 9 = mountain mahogany

other Sky Islands. Other possible explanations for the higher species richness in CHIR relative to the Santa Catalina Mountains could relate to area and location effects. The Chiricahua Mountain range is the larger of the two mountain masses and is also closer to the very diverse Sierra Madre Occidental proper than the Santa Catalina Mountains and supports more species from this major mountain range.

Beta diversity

Rapid changes in elevation and topography over short distances in CHIR resulted in high species turnover (β -diversity) due to abrupt shifts in local site conditions and shifts from low to high elevations. β -diversity in CHIR was greatest at high altitudes as terrain became more broken and incised with increasing elevation. The topographic complexity potentially responsible for high α -diversity in CHIR may have also contributed to rapid species turnover along the environmental gradients of elevation and soil moisture. The topography in CHIR is much more complex than many other mountain ranges in the western United States (Coblentz and Riitters 2004, 2005), and β -diversity is high compared to other mountain ranges in Arizona, the Rocky Mountains, and elsewhere (Whittaker and Niering 1965; Peet 1974; Allen et al. 1991; Pitkänen 2000; Oliver

et al. 1998; White and Hood 2004), which suggests that vertical species stacking in CHIR may be greater than in other areas.

Gamma diversity

Sky Island ecosystems are often considered to be biodiversity hotspots because of their uniqueness in an otherwise desert landscape (DeBano et al. 1995). However, woody plant species richness in Sky Island Mountains is intermediate in comparison to other vegetated regions of the world. Landscape-scale species richness (γ -diversity) in CHIR is higher than many other temperate forests including the high latitude forests in Finland (Pitkänen 2000), the high altitude forests of the Rocky Mountains (Allen et al. 1991), the Great Smoky Mountains (Whittaker 1956), the Siskiyou Mountains (Whittaker 1965), the low elevation pine barrens of Wisconsin (Brososke et al. 1999), and the Australian mallee woodlands of New South Wales (Whittaker et al. 1979). However, mid-elevation and upland forests of the Colorado Front Range (Peet 1978, 1981) and eucalypt forests of New South Wales (Oliver et al. 1998) have higher γ -diversity than CHIR. Furthermore, tropical systems have dramatically higher species richness (Chazdon et al. 1998; Williams-Linera 2002).

Stand structural diversity

Our analysis of stand structural diversity patterns in CHIR demonstrates that the most species rich vegetation types are not necessarily the most structurally diverse. While juniper-oak forests have high species richness, they are open woodlands with mainly intermediate sized trees and subsequently intermediate structural diversity. In contrast, gallery forests are heavily shaded, thus excluding shade intolerant species. They have fewer species, but have greater structural complexity (i.e., size-classes), which provides key habitat for wildlife. Many birds prefer closed canopy forest to open woodland, and there appears to be a tight relationship between habitat structure and bird species composition (Morse 1985; DeGraaf et al. 1998). This pattern suggests that while α - and β -diversity measures are important in terms of quantifying plant species richness and turnover, stand structural complexity is an important measure that should be included in landscape-scale diversity studies.

Conclusions

Elevation, heat load, soil moisture, and soil type are the primary controls on species distribution patterns, species diversity, and woody plant structure in Arizona Sky Island Mountains. Elevation is the most important environmental factor influencing woody plant community composition and structure, though the independent effects of heat load, soil moisture, and soil type also play important roles. Species complexes and plant life-form types sort similarly in CHIR and other mountain ranges in the Southwest. Local site conditions have a strong influence on structural complexity by controlling the range of species and size of individuals on a particular site. For example, vegetation on harsh sites (i.e., shallow soils, high heat loads, low soil moisture) is less structurally complex whereas better sites (i.e., mesic, alluvial soils) support structurally stratified gallery forest. Woody plant diversity in the Southwestern mountains is highest in open woodland vegetation types that span wide elevational ranges, and the fact that these vegetation types are the most species rich, rather than more structurally complex gallery

forest types, has important implications for forest and wildlife management. The rapid species turnover (β -diversity) along elevation and soil moisture gradients in the Madrean Archipelago is most likely related to the high topographic complexity of these mountains relative to other ranges. The large elevation gradients and broken topography in these mountains have resulted in vertical stacking and mixing of species. These mountains are highly diverse in comparison to lowland vegetation types (i.e., mesquite covered grasslands and creosote dominated desert), making them regional biodiversity hotspots for the desert Southwest.

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