

Mountaintop island age determines species richness of boreal mammals in the American Southwest

Jennifer K. Frey, Michael A. Bogan and Terry L. Yates

J. K. Frey (jfrey@nmsu.edu) and T. L. Yates, Museum of Southwestern Biology and Dept of Biology, Univ. of New Mexico, Albuquerque, NM 87131, USA (present address of J. K. F.: Dept of Fishery and Wildlife Sciences, and Dept of Biology, New Mexico State Univ., P.O. Box 30003, Campus Box 4901 Las Cruces, NM 88003-0003, USA). – M. A. Bogan, U. S. Geological Survey, Museum of Southwestern Biology, Univ. of New Mexico, Albuquerque, NM 87131-0001, USA.

Models that describe the mechanisms responsible for insular patterns of species richness include the equilibrium theory of island biogeography and the nonequilibrium vicariance model. The relative importance of dispersal or vicariance in structuring insular distribution patterns can be inferred from these models. Predictions of the alternative models were tested for boreal mammals in the American Southwest. Age of mountaintop islands of boreal habitat was determined by constructing a geographic cladogram based on characteristics of intervening valley barriers. Other independent variables included area and isolation of mountaintop islands. Island age was the most important predictor of species richness. In contrast with previous studies of species richness patterns in this system, these results supported the nonequilibrium vicariance model, which indicates that vicariance has been the primary determinant of species distribution patterns in this system.

One of the most fundamental questions about the biogeography of a system is whether distribution patterns resulted from dispersal or vicariance. Dispersal is the movement of an organism across a barrier to colonize a new area, while vicariance is the fragmentation of a formerly continuous distribution into smaller, isolated portions. Due to inherent philosophical and methodological differences, these distributional mechanisms have largely defined major subdisciplines of biogeography: ecological biogeographers favoring dispersal scenarios and historical biogeographers favoring vicariance scenarios (Udvardy 1981). The evaluation of species richness patterns is a common macroecological method that bears on this question in insular systems. Various species richness patterns are predicted from competing alternate theoretical models of insular system dynamics. In turn, these models provide explanations for the mechanisms that have resulted in contemporary species distribution patterns.

The models

Under the equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) species richness on an island is a dynamic equilibrium between opposing rates of colonization and extinction. It is assumed that the rate of colonization is determined by island isolation such that the rate of colonization is reduced with increasing isolation. Similarly, it is assumed that island area determines the rate of extinction such that the rate increases on smaller islands. Consequently, in an equilibrium system, species richness should exhibit a significant negative relationship with isolation and a significant positive relationship with area (Fig. 1). These results would indicate that dispersal must be occurring.

The alternative model, which we will call the nonequilibrium vicariance model, assumes that vicariance results in isolation of islands through fragmentation of a formerly contiguous area containing the total

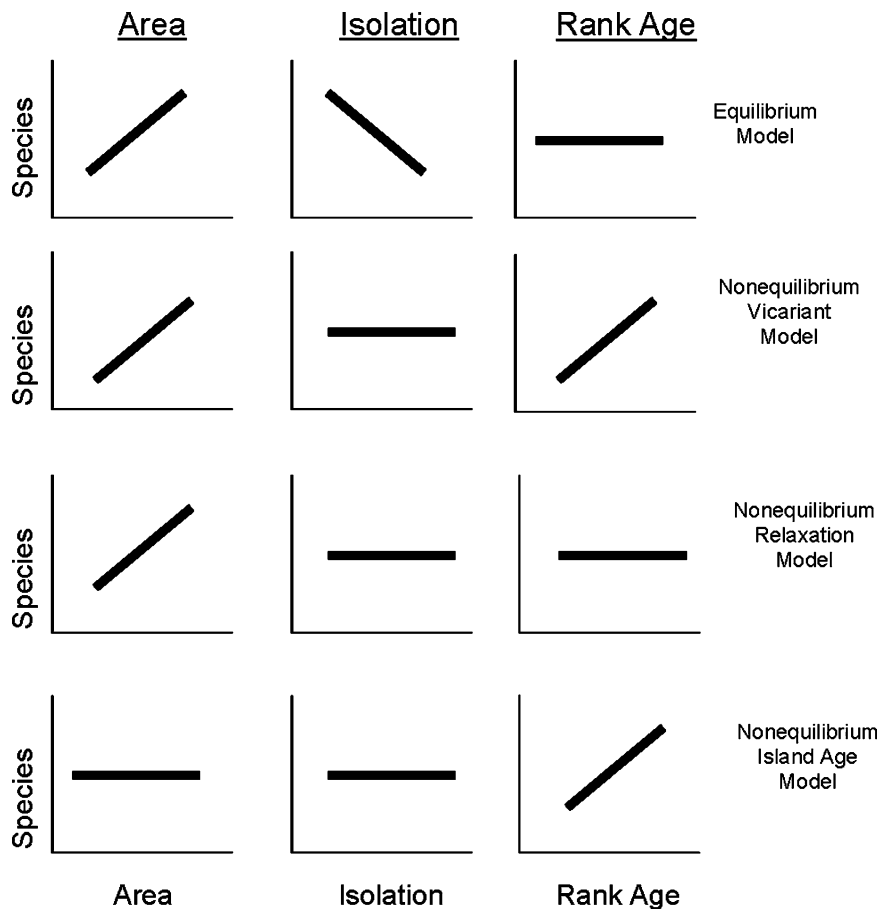


Fig. 1. Predicted relationships (i.e. slope of the regression line) between species richness and island attributes based on alternative island biogeographic models. Rows represent alternative models including the equilibrium theory of island biogeography, the nonequilibrium vicariance model, and special cases of the nonequilibrium vicariance model, the relaxation model and the island age model. Columns represent island attributes including area, isolation, and age.

species pool. Thus, at fragmentation these “landbridge” islands start with the pool number of species but subsequent extinction results in a decline in species richness through time. In this model both area and age of the island determine the rate of extinction. Like the equilibrium model, it is assumed that area is a determinant of the rate of extinction. However, island age is also a determinant of rate of extinction, such that species richness would be lowest on the island formed first because of a longer opportunity for extinction to erode the original species pool while species richness would be highest on the most recently formed island because there would be less time for stochastic processes to lead to extinction. Unlike the equilibrium model, there is no dispersal that can reestablish populations. Consequently, a nonequilibrium vicariant system predicts a significant positive relationship between species richness with area (as in the equilibrium system), a significant positive relationship between species richness

with age (arranged oldest to youngest), but no significant relationship between species richness and isolation (Fig. 1). These results would indicate that dispersal must not be occurring and that distribution patterns are solely the product of vicariance.

Brown’s (1971, 1978) nonequilibrium relaxation model was the original precursor to the nonequilibrium vicariance model. The relaxation model specified that area and its attendant extinction rate was the only determinant of species richness; time was but an implicit consideration in the model. Thus, the relaxation model is but a special case of the vicariance model wherein island age has no influence on species richness or wherein the islands were formed at the same time (Fig. 1). An alternative model, which we call the island age model, has time as an explicit consideration in that island age is the sole determinant of species richness. Thus, the island age model is also but a special case of the vicariance model wherein island area

has no influence on species richness or wherein the islands have the same area (Fig. 1). Although island age has been shown to be an important predictor of species richness patterns in some oceanic systems (Wilcox 1978, Crowell 1986, Borges and Brown 1999), analyses involving island age remain relatively rare. This may be because age is a difficult, or seemingly impossible, variable to collect for many types of insular systems.

Study objectives

The American Southwest has been the focus of many studies that have attempted to determine the primary mechanisms accounting for contemporary distribution patterns of montane mammals. In this system, it is presumed that continuous boreal coniferous forest habitats were fragmented through post-Pleistocene warming that resulted in the retraction of these cold-adapted forests from the lowest elevations until they became isolated on mountaintop refugia (Lomolino et al. 1989, Harris 1990). This process probably occurred through several episodes of expansion and contraction that variously influenced dispersal rates among islands. While the vicariant formation of these mountaintop islands of boreal habitat is generally not argued, the subsequent distributional dynamics of mammals inhabiting these islands has been debated. Proponents of dispersal maintain that intermountain dispersal, perhaps primarily through lower elevation conifer woodland corridors, has been an important force mediating contemporary species distribution patterns and that the system is consistent with the equilibrium theory (Davis et al. 1988, Lomolino et al. 1989, Lomolino and Davis 1997). This view has become a paradigm of how climatic processes have structured contemporary insular communities. In contrast, proponents of vicariance maintain that little or no intermountain dispersal occurs and the system is consistent with a nonequilibrium vicariance model (Findley 1969, Patterson 1980, 1982, 1984, 1995, 1999, Sullivan 1994).

Although many of the previous studies included an evaluation of traditional species richness patterns, age of the islands has not been included as a variable in this or any other continental mountaintop system. Thus, the overall goal of this study was to assess whether contemporary distribution patterns of boreal mammals in the American Southwest are a product of dispersal or vicariance by testing between the competing models through evaluation of species richness patterns. Besides the traditional evaluation of species richness in light of island area and isolation, this study provides the first attempt to evaluate species richness patterns in light of island age by combining techniques from both ecological and historical biogeography.

Methods

Mountain ranges

The study area included that portion of the American Southwest south of 37.5°N latitude and the Colorado River. Lawlor (1998) noted that it is necessary to define mountaintops and their characteristics appropriately in order to distinguish between biogeographic signal and noise. In this study, the mainland and mountaintop islands were defined as areas of Petran subalpine conifer forest (PSCF) based on the map of Brown and Lowe (1980), which best represented the distribution of the boreal mammal fauna. This forest community is dominated by Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa*; Brown 1994. With the exception of alpine tundra, PSCF occurs at the highest elevations and is the most geographically restricted montane community in the Southwest. This resulted in the inclusion of the Southern Rocky Mountains mainland (combined San Juan and Sangre de Cristo ranges) plus 18 mountaintop islands south of the mainland (Fig. 2). Although most islands consisted of a single area of PSCF, five included two or more areas of PSCF. In these cases, the area of all PSCF on a mountain range was considered together. Allegres Mountain (Catron County, NM) was excluded because there has been no mammal inventory.

Mammal focal species

Inclusion of species with different histories can obscure biogeographic patterns (Patterson 1995, 1999). For example, Patterson (1999) found that for montane mammals in the American Southwest, groups of species with different histories exhibited dramatically different biogeographic patterns. Consequently, we only included those terrestrial mammal species that exhibit a significant affinity for PSCF and upper Petran montane conifer forest (MCF) in the Southwest, have northern geographic affinities, and occur on at least one island. MCF is a mid-elevation forest of two types, including mixed conifer forest at higher elevations, which are dominated by Douglas fir *Pseudotsuga menziesii*, white fir *Abies concolor*, and southwest white pine *Pinus strobiformis*, and a lower elevation more arid ponderosa pine *Pinus ponderosa* forest (Brown 1994). Below MCF are non-forest communities, including Great Basin conifer woodland (GBCW) at the highest elevations, which is dominated by piñon pine (*Pinus*) and juniper (*Juniperus*), and is often considered a filter-barrier for boreal mammal dispersal (Lomolino et al. 1989, Brown 1994). Below GBCW are various grassland and desert communities, which are considered more substantial barriers to dispersal for montane mammals.

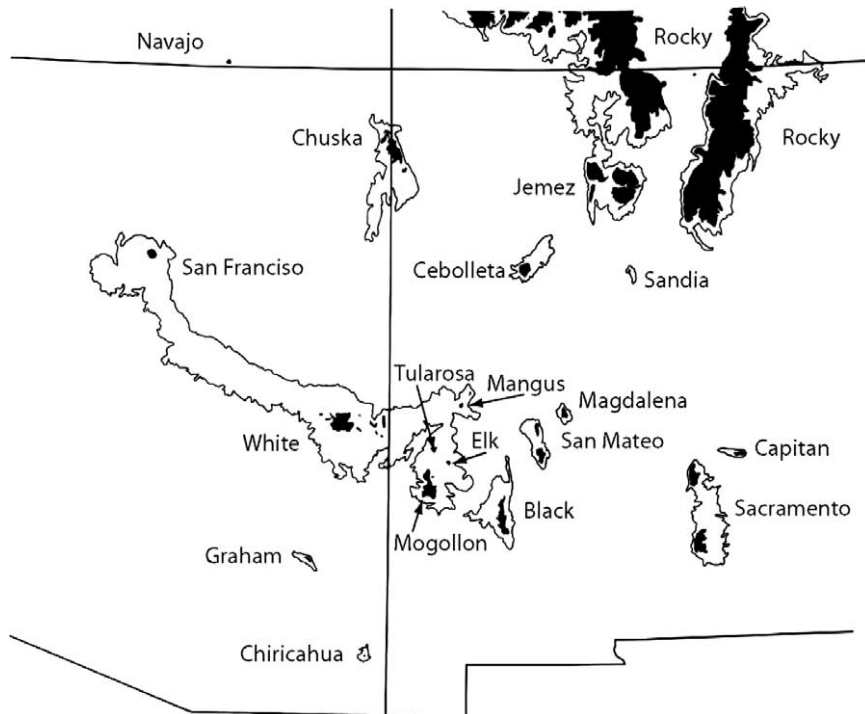


Fig. 2. Islands of Petran subalpine coniferous forest (black areas) in the American Southwest (adapted from Brown and Lowe 1980). Contour lines are the lower edge of Petran montane conifer forest. The Rocky Mountain boreal forest extends northward in Colorado.

According to data presented in Lomolino et al. (1989) all but two species included in this study had the vast majority of Southwest occurrence records in mixed conifer and PSCF. The two exceptions were the chipmunks, *T. minimus* and *T. quadrivittatus*, which are not uncommon in GBCW, particularly in the northern areas of the Southwest (especially the mainland). However, lower latitude insular populations of these species tend to be more restricted to mixed conifer and PSCF (Findley et al. 1975). Species excluded from the analyses were *Sorex nanus* and *S. preblei* because of poor distribution data, *Sorex cinereus* because the record of this species in the Jemez Mountains (Findley et al. 1975) is possibly *S. preblei* or *S. haydeni* (Demboski and Cook 2003, J. Findley pers. comm.), and *Neotoma cinerea* because one subspecies (*N. c. arizonae*) occurs primarily in GBCW. This resulted in the inclusion of 14 boreal mammal species (Table 1).

Presence of each species on each island was determined from published sources and from our own surveys. Mammal surveys were conducted in all of the included ranges although these were more concentrated on mountain ranges that had received little or no prior survey effort. Surveys were designed to document maximum species richness using a variety of standard field techniques (Wilson et al. 1996). Voucher speci-

mens were deposited in the Museum of Southwestern Biology, Univ. of New Mexico.

Measurements of area, isolation, and age

Estimates of area and isolation were measured from the Brown and Lowe (1980) map (Table 2). Area (A) of each PSCF habitat patch was determined using a polar planimeter. Other higher elevation habitat types (e.g. tundra, subalpine grassland) were included in this measure. Isolation can be measured in many different ways (Lomolino et al. 1989, Floyd et al. 2005). We measured isolation (I) as the shortest straight-line distance from an island to the Rocky Mountain mainland because similar straight-line measures have been used in previous studies of montane mammal biogeography in the American Southwest (Lomolino and Davis 1997).

The rank age (V) of each island was determined based on a presumed pattern of vicariant disjunction of boreal habitat (Table 2). A vicariant model in the form of a geographic cladogram was constructed in a manner similar to Sullivan (1994). We assumed that habitats suitable to all species connected all contemporary islands in the past and that subsequent climatic warming and drying resulted in the retraction of these

Table 1. Species occurrences of boreal mammals in the American Southwest^a.

Species	Mountain Range ^b														Occupied ranges			
	JEM	WHI	CHU	SAN	MOG	CEB	TUL	BLA	SFR	SAC	SMA	ELK	MAN	GRA		MAG	CAP	NAV
<i>Tamiasciurus hudsonicus</i>	1	2	1	1	1	1	3	1	2	1	1	1	3	2	1	1		15
<i>Sorex monticolus</i>	1	2	1	1	1	1	3	1	2	1	1	1	3	2	1		2	14
<i>Microtus longicaudus</i>	1	2	1	1	1	1	3	1	2	1	1	3	3	2	1	1		13
<i>Spermophilus lateralis</i>	1	2	1	1	1	1	1	1	2	1	3	3	3	2				9
<i>Clethrionomys gapperi</i>	1	2	1		1		3				1				1			6
<i>Tamias minimus</i>	1	2	1	1	1					1								5
<i>Tamias quadrivittatus</i>	1		1	1	1	1												4
<i>Sylvilagus nuttallii</i>	1	2	1	1										2				4
<i>Thomomys talpoides</i>	1	2	1	1	1	1												3
<i>Sorex palustris</i>	1	2																2
<i>Microtus montanus</i>	1	2																2
<i>Mustela erminea</i>	1			1														2
<i>Martes americana</i>	4																	1
<i>Ochotona princeps</i>	1																	1
Species per range	14	9	8	6	5	5	5	4	4	3	3	3	3	3	2	2	1	1

^aRecords are from: 1, Findley et al. (1975); 2, Hoffmeister (1986); 3, this study; 4, C. Painter pers. comm.

^bAbbreviations are defined in Table 2.

habitats to higher elevation refugia that maintained suitable climate. Historically suitable habitat might have consisted of different vegetation associations because species move independently rather than as unified communities (Harris 1990, Dick-Peddie 1993). Further, fossil evidence suggests that this connection of suitable habitat extended to all of our mountaintops, except the Graham and Chiricahua mountains, at least during the Wisconsin (Harris 1990). Because elevation is a primary determinant of vegetation, Sullivan (1994) utilized topographic contours to assess the sequence of isolation of forested areas. In contrast, we used the contour of the lower limit of biotic communities as mapped by Brown and Lowe (1980) to determine the basic structure of the geographic cladogram. Biotic communities were used because vegetation patterns reflect the idiosyncratic characteristics of all landscape features including elevation, latitude, shape and position of topographic features, air currents, and aspect. These idiosyncratic characteristics would be preserved under different climate regimes.

We used relative temperature equivalents of valleys separating the mountaintop islands within a particular biotic community contour to further refine the branching sequence. Although precipitation and seasonality also influence vegetation, temperature has a primary influence on vegetation type and is related to both elevation and latitude. Thus, the temperature equivalent was set in relation to a hypothetical valley located at 34°N latitude, 6500 feet (1981 m) elevation with a mean annual temperature of 54°F (12.2°C); approximate averages in New Mexico. Temperature equivalents were calculated utilizing temperature lapse rates specific to Arizona (Lowe 1964): 1°F (0.56°C) per 1° latitude and 1°F (0.56°C) per 250 feet (76 m) elevation. Thus, the temperature equivalent (TE) was calculated, $TE = 54 + [(6500 - E) / 250] + [34 - L]$, where E is the lowest elevation (in feet) and L is the latitude of the lowest elevation point of the valley. Valley latitude and elevation was determined using Topo USA 3.0 (Anon. 2001). From the geographic cladogram, the rank order (i.e. rank age) that each island was separated from the Rocky Mountains mainland was determined. For rank age, small numbers are older events as opposed to actual age where small numbers are younger events. The rank order of internal clades was averaged to produce the resulting branching sequence (Fig. 3).

Statistical analyses

Normality of variables was assessed visually using box plots and histograms and statistically using one-sample Kolmogorov-Smirnov tests. Age was non-normal and

Table 2. Biogeographic attributes of mountaintop islands of boreal forest in the American Southwest.

Mountain Range	Abbreviation	Area (km ²)	Isolation (km)	Rank age	Species richness
Jemez	JEM	857.0	30	18.5	14
White	WHI	314.7	351	13.5	9
Chuska	CHU	239.3	131	9.0	8
Sandia	SAN	4.0	72	5.0	6
Mogollon	MOG	190.2	347	13.5	5
Cebolleta	CEB	108.2	159	13.5	5
Tularosa	TUL	16.4	329	13.5	5
Black	BLA	196.7	318	13.5	4
San Francisco	SFR	59.0	381	13.5	4
Sacramento	SAC	297.2	229	5.0	3
San Mateo	SMA	104.9	243	8.0	3
Elk	ELK	16.4	328	13.5	3
Mangus	MAN	9.8	281	13.5	3
Graham	GRA	9.8	493	1.5	3
Magdalena	MAG	52.5	215	7.0	2
Capitan	CAP	16.4	219	5.0	2
Navajo	NAV	4.0	237	3.0	1
Chiricahua	CHI	3.0	524	1.5	1

transformations did not improve normality. Area and species richness were log transformed. Isolation, $\ln(\text{area})$, and $\ln(\text{species richness})$ were deemed normal. Statistical analyses, which included correlations, partial correlations, linear regressions, and multiple regressions, were performed using SPSS for Windows version 11.5 (Anon. 2002).

Results

Among the independent variables, the only significant correlation was between area ($\ln[A]$) and rank age ($r_s = 0.586$; $p = 0.011$). Significant relationships between the independent variables and species richness (as $\ln[S]$) existed for area (power model $S = 0.267A^{0.269}$;

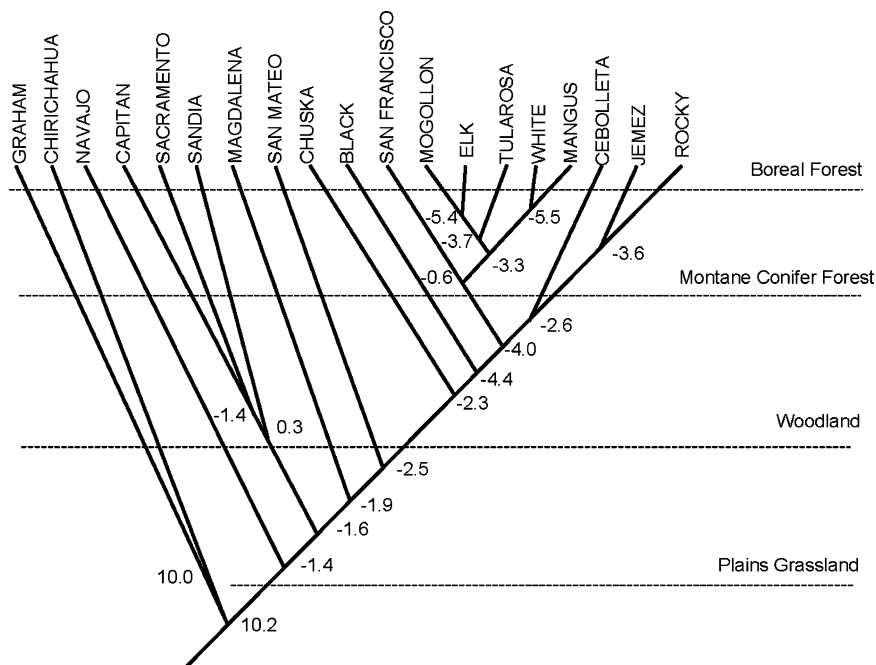


Fig. 3. Geographic cladogram of the pattern of vicariant disjunction of boreal habitat (i.e. Petran subalpine conifer forest) in the American Southwest. Dashed lines represent the biotic community shared by each clade. Numbers besides nodes are temperature equivalents of the valley separating the corresponding clades.

$r = 0.678$; $p = 0.002$) and age (regression model $\ln[S] = 0.402 + 0.093[V]$; $r_s = 0.653$; $p = 0.003$), but not for isolation (regression model $\ln[S] = 1.954 - 0.002[I]$; $r = -0.461$; $p = 0.054$). Based on partial correlations, species richness and area were significantly correlated when corrected for the effects of isolation ($r_{-I} = 0.623$, $p = 0.008$), but not when corrected for the effects of age ($r_{-V} = 0.458$, $p = 0.064$) or the effects of both age and isolation ($r_{-I \text{ and } V} = 0.402$, $p = 0.123$). In contrast, species richness and rank age were significantly correlated when corrected for the effects of area ($r_{-A} = 0.491$, $p = 0.045$), isolation ($r_{-I} = 0.672$, $p = 0.003$), and both area and isolation ($r_{-A \text{ and } I} = 0.499$, $p = 0.049$). When corrected for influence of area and age, all relationships between species richness and isolation were nonsignificant ($p > 0.1$).

A stepwise multiple regression resulted in age as the only significant ($p = 0.001$) predictor of species richness. A backward multiple regression eliminated isolation as a significant predictor (regression model $\ln[S] = 0.096 + 0.60[V] + 0.163[\ln(A)]$; $r = 0.768$; $p = 0.001$) as compared to one including all three independent variables (regression model $\ln[S] = 0.562 + 0.058[V] + 0.135[\ln(A) - 0.001[I]$; $r = 0.799$; $p = 0.002$). In both of these multiple regression models, age was the only significant coefficient ($t = 2.157$, $p = 0.049$ for the model including A, I, and V; $t = 2.186$, $p = 0.045$ for the model including A and V).

Discussion

Patterns of species richness strongly supported predictions of the nonequilibrium vicariance model. Simple regressions revealed highly significant relationships ($p \leq 0.003$) between species richness with island area and island age. These statistical patterns were generally maintained in partial correlations that corrected for influence of other independent variables. In contrast, while the simple correlation between island isolation and species richness was marginally significant ($p = 0.054$), the relationship was highly nonsignificant ($p > 0.1$) when controlled for area and age. Further, isolation was not a significant variable in either the stepwise or backward regressions. Results of the stepwise regression indicated that age was the most significant predictor of species richness. The nonsignificant partial correlation between area and species richness when controlling for age and the nonsignificance of area as a coefficient in the backward multiple regression further indicated that age was a stronger influence as compared with area. It is possible that the significant correlation between age and area could confound interpretation of the relative importance of each of these variables in determining species richness.

Regardless, the strong influence of both area and age relative to a very weak or absent influence from isolation clearly supported vicariance as the process shaping insular distribution patterns. In contrast, there was no support for the equilibrium model, which requires dispersal as a key mechanism for structuring species richness patterns.

Results of this study are dramatically different from previous studies of species richness patterns in montane mammals of the American Southwest. All previous studies of this system that included an analysis of both species-area and species-isolation relationships found that patterns were consistent with predictions of the equilibrium model (Davis et al. 1988, Lomolino et al. 1989, Lomolino and Davis 1997). Part of the reason for the conflicting results may be due to differences in how the archipelago was defined. Earlier studies defined islands based on MCF, which is a more arid adapted forest found at lower elevations than PSCF. Although the MCF includes the higher elevation mixed conifer forest, which is generally suitable for boreal species, the lower elevation ponderosa pine forest is generally unsuitable for boreal species. Consequently, use of MCF to define islands tends to overestimate island area and underestimate island isolation while use of PSCF is a more conservative approach because it tends to underestimate island area and overestimate island isolation.

Second, this study included virtually all of the insular areas of PSCF in the archipelago. In contrast, earlier studies only included a subset of the largest islands. Small islands have been shown to exhibit weak species-area relationships relative to large islands (i.e. small island effect; Morrison 1997, Brown and Lomolino 1998, Lomolino and Weiser 2001). Thus, exclusion of small islands in previous studies could have resulted in a steeper species-area relationship. Further, because area and isolation were correlated in previous studies ($r_s = -0.462$, $p = 0.015$ for untransformed data in Davis et al. 1988; $r = -0.014$, $p = 0.014$ using $\ln[\text{area}]$ in Davis et al. 1988; $r_s = 0.691$, $p = 0.000$ for untransformed data in Lomolino et al. 1989; $r = -0.715$, $p = 0.000$ using $\ln[\text{area}]$ in Lomolino et al. 1989), this would translate into correspondingly steeper slopes of the species-isolation relationship making the system appear consistent with the equilibrium model.

Species included in this and earlier studies differed. With one exception (*Sylvilagus nuttallii* and *Tamias quadrivittatus* were not included in Davis et al. [1988]), earlier studies included all species that were used in this study. However, this study included a smaller fauna due to the exclusion of species for various reasons. In addition, this study utilized a more complete species occurrence matrix based on field surveys, in addition to the literature records used in previous studies. Finally,

errors in species occurrence were found in Lomolino and Davis (1997; e.g. *Lepus americanus* was recorded as present in the Mogollon forest site, *Clethrionomys gapperi* was not recorded as present in the Magdalena or San Mateo forest sites).

The models differ in predictions about the nature of the species-area relationship. Using log-transformed variables, this relationship is usually reported as the power function, $S = cA^z$, where S is species richness, A is area, c is a fitted constant equivalent to the y -intercept, and z is a fitted constant equivalent to the slope. Lomolino (1989) warned that comparisons of z -values should be made with caution because z -values do not, by themselves, indicate how rapidly species richness increases with area on an arithmetic scale (Lomolino 1989). Despite this, z -values are often compared and usually interpreted as representative of the degree of dispersal in a system. For example, islands generally have higher z -values than similar sized areas of contiguous habitat (Brown and Lomolino 1998) and landbridge islands have z -values typically twice as great as those for oceanic islands (Lawlor 1986).

Results indicate that the common interpretation of z -values as representative of the degree of dispersal in a system may not be accurate for all systems. For example, previous studies concluded that the Southwest montane mammal system was consistent with the dispersal-driven equilibrium theory even though they exhibited higher z -values than that found in this study ($z = 0.273$; $SE = 0.073$), which was based on an archipelago and fauna with more restrictive opportunity for dispersal. Second, if more dispersal results in lower z -values, then systems conforming to the equilibrium theory should have lower z -values than systems conforming to the vicariance model. This may not necessarily be the case because in the vicariance model extinction rates are determined by both island area and age. If age is the strongest determinant of species richness, then it is possible for these systems to exhibit relatively low z -values. The relaxation model was developed to explain distribution patterns of montane mammals in the Great Basin (Brown 1971, 1978). However, a continual reduction in z -value with each reanalysis ultimately contributed to the rejection of the relaxation model in support of the equilibrium theory (Lawlor 1998). High levels of genetic diversity and a correlation between genetic and geographic distance in yellow-bellied marmots *Marmota flaviventris* also seemingly supported this conclusion (Floyd et al. 2005). However, these conclusions may have been premature given that the influence of island age has not been tested in that system, especially if age proves to be a correlate of island isolation.

MacArthur and Wilson (1967) noted that a strong test for equilibrium is a situation in which $\ln(S)$ increases with area more rapidly on more isolated islands than on

islands nearer the mainland. This test was seemingly fulfilled for the southwest montane mammals. The nine islands nearest to the mainland had a non-significant species-area relationship ($r = 0.608$; $p = 0.082$; $S = 0.235A^{0.261}$), while the nine islands furthest from the mainland had a significant positive species-area relationship ($r = 0.813$; $p = 0.008$; $S = 0.239A^{0.295}$). These results are seemingly at odds with conclusions based on species richness patterns for the entire system. However, correlations among the independent variables contributed to these results. Island age exhibited a significant negative correlation with isolation for the furthest islands ($r_s = -0.725$, $p = 0.027$) and a significant positive correlation with area for the nearest islands ($r_s = 0.715$, $p = 0.030$). Although the species-area relationship for the furthest islands remained significant when controlled for isolation ($r_{-I} = 0.745$, $p = 0.034$), it was not significant when controlled for age ($r_{-V} = 0.670$, $p = 0.069$) or both age and isolation ($r_{-V \text{ and } I} = 0.669$, $p = 0.100$). Second, the species-area relationship of the nearest islands remained nonsignificant when controlled for age ($r_{-V} = 0.123$, $p = 0.771$), but became significant when controlled for isolation ($r_{-I} = 0.839$, $p = 0.009$) and both age and isolation ($r_{-V \text{ and } I} = 0.769$, $p = 0.043$). Thus, the observed species-area relationship was inflated for the furthest islands and depressed for the nearest islands.

A second reason for the non-significant species-area relationship of the nearest islands was due to the influence of the Sandia Mountains. Of the 18 islands, this mountain was most supersaturated based on area (standard residual = 2.208) and age (standard residual = 1.809), but was not an outlier based on isolation (standard residual = 0.023). Thus, the species-area relationship of the nearest islands is nearly significant if richness in the Sandia Mountains is reduced by one ($r = 0.658$, $p = 0.054$, $S = -0.145A^{0.278}$) and highly significant if the island is excluded ($r = 0.888$, $p = 0.003$, $S = -0.704A^{0.439}$). When this island was excluded, the species-area relationship remained significant ($p < 0.05$) when corrected by partial correlations for any subset of independent variables. The removal of other islands did not result in a significant species-area relationship of the nearest islands. This pattern is likely due to a potentially erroneous observational record of *Mustela erminea* in the Sandia Mountains (Ivey 1957). Specimens or additional observations have not substantiated this observation and this is the only species reported from the Sandia Mountains that has not been reported from other mountains within the same woodland contour.

We conclude that the pattern of species-area relationships for near versus far islands is not consistent with predictions of the MacArthur and Wilson (1967) equilibrium test. Rather, we found that by controlling for the influence of the Sandia Mountains or correlations among independent variables, both groups of

islands had significant species-area relationships. This pattern is expected under the nonequilibrium vicariance model.

Many previous studies also concluded that montane mammals in the American Southwest represent a nonequilibrium system produced through vicariance with little or no contemporary intermountain dispersal (Findley 1969, Patterson 1980, 1982, 1984, 1995, 1999, Sullivan 1994). Those studies used a variety of techniques and rationales, typically of a historical nature, in generating their conclusions, but generally did not include analyses of species richness patterns. In contrast, previous studies that concluded that this system was consistent with the equilibrium theory utilized species richness patterns as a primary source of evidence (Davis et al. 1988, Lomolino et al. 1989, Lomolino and Davis 1997). This study provides a bridge between the alternative types of studies by inclusion of techniques from both historical and ecological biogeography. In addition, the use of age as a variable provided a third dimension which was able to provide better resolution of the factors responsible for shaping species distribution patterns.

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