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## TOPOGRAPHIC MODELS OF VASCULAR PLANT RICHNESS IN THE SOUTHERN APPALACHIAN HIGH PEAKS

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### SUMMARY

(1) Data from a vascular plant survey of the southern Appalachian high peaks, U.S.A., were used to model the relationship between five floristic categories of species richness (total, high elevation, northern, endemic and rare species), six topographic variables (area above 1680 m, area above 1830 m, maximum elevation, number of peaks, inter-mountain distance and latitude) and the number of community types.

(2) The best model of species richness varied with each richness category: total richness was best modelled by number of communities, high elevation species by area, northern species by area, endemic species by number of communities and rare species by maximum elevation.

(3) In simple regressions, there was no clear preference among model formulations or species richness transformations. Elevation, number of peaks and area were all relatively important predictors, while isolation was unimportant. In multiple regression models, linear formulations were almost always the strongest. For total species richness, the best multiple regression model was linear and the most important predictor was the number of peaks.

(4) Rare species richness increased faster with area or elevation than any other richness category (slope coefficients for log (rare species)—log (area) models were 0.30 for the whole data set and 0.49 for the eight largest areas).

(5) Distance between mountains almost always had a positive, though usually minor, effect on species richness, thus casting doubt on the appropriateness of the MacArthur and Wilson model for this data set. We hypothesize that distance between mountain areas is probably a poor measure of ecological isolation and that historic extinctions have shaped the species–area relations we observed.

### INTRODUCTION

Studies of mountain-top floras and faunas have found strong correlations between the area defined by an elevational contour and species richness above that contour (Billings 1977; Brown 1971; Johnson 1975; Riebesell 1982; Vuilleumier 1970). However, area may not be as strong a predictor of species richness as is elevation (Thompson 1978) or habitat heterogeneity (Behle 1978; Kitchener *et al.* 1980). Distance between mountain tops may also influence richness (Riebesell 1982).

Ten southern Appalachian mountain ranges in the south-eastern United States reach 1680 m, the requisite elevation for transition from deciduous broad-leaved forest to evergreen spruce (*Picea*) and fir (*Abies*) forests at this latitude (35–37°N). The spruce–fir

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forests of these mountains are isolated by 1000 km from the well developed spruce–fir forests of the northern Appalachians. We have described the floristic patterns and correlations between total richness and area elsewhere (White, Miller & Ramseur 1984). Here, we address the formal aspects of the relationship between species richness and various topographic variables. Three kinds of hypotheses were tested: (i) area is the best predictor of species richness; (ii) log–log formulations of species–area models have higher coefficients of determination than do linear or semi-log formulations (Connor & McCoy 1979); and (iii) log-transformed richness is a better formulation than is untransformed richness or species fraction (Schoener 1976).

A second reason for extending our earlier analysis derives from distribution of high elevation rare species in these mountains. The area available to cool climate species in the study area has fluctuated during the last 20 000 years (Delcourt & Delcourt 1979). Spruce–fir forests were found below 1000 m at 18 000 years before present. With climatic warming, these forests became progressively fragmented and restricted to the highest elevations, reaching their most restricted distribution at 5000 years before present, when they were displaced upward (compared to present distributions) by an estimated 70–150 m (Whittaker 1956). As an extension of Whittaker's (1956) hypothesis concerning the absence of spruce–fir from certain slopes in our study area, we developed the working hypotheses that the number of extinctions on each mountain mass was a function of area above a critical contour (1830 m), and that rare species restricted to high elevations would be strongly correlated with area above 1830 m and would show a steep species–area relationship. In this analysis we used four subsets of total floristic richness: northern species (species at their southern range limit), endemic species (species restricted to the southern Appalachian high mountains), high elevation species (northern plus endemic species) and rare species (high elevation species that occur in low abundance).

## METHODS

Mountain-top area was defined planimetrically on topographic maps (White, Miller & Ramseur 1984). Five of the ten ranges had more than one peak above the 1680 m contour. This characteristic will be referred to below as 'number of peaks'. Other topographic characteristics considered were area (above the 1680 m and 1830 m contours), maximum elevation, isolation (distance to the nearest range surpassing 1680 m), and latitude. A final variable characterizing the mountain ranges was the number of community types present. The full data set is presented in Appendix 1, which is compiled from White, Miller & Ramseur (1984), except for the additions of area above the 1830-m contour and transformed richness data. Simple and multiple least-squares regression analysis was used to formulate equations predicting species richness from topographic data and number of community types.

## RESULTS

### *Single variable regressions of log-transformed richness*

We examined the relationship of total and high elevation species richness to area and tested the strength of the log-transformed area model against other single variable models (Table 1). Examination of model residuals suggested that the two smallest areas in the data set were outliers (i.e. they had higher richness than would be expected based on their

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TABLE 1. Simple linear regression equations log-transformed richness variables. For each variable, the equations are listed by number of areas included (10 = the whole data set; 8 = the eight largest areas) and then by decreasing coefficients of determination ( $r^2$ ). Equations are only listed if  $P > F$  was  $\leq 0.05$ .

Dependent variable	Independent variable	Number of areas in data set	Intercept	Slope	$r^2$	Level of significance $P > F$
Log (total richness)	Communities	10	1.7	0.07	0.68	0.05
	Number of peaks	10	1.9	0.03	0.62	0.01
	Elevation	10	-0.2	0.002	0.48	0.05
	Log (area)	10	2.0	0.12	0.40	0.05
	Log (area)	8	1.8	0.28	0.84	0.005
	Communities	8	1.6	0.10	0.67	0.01
	Number of peaks	8	1.9	0.03	0.67	0.01
	Elevation	8	-1.4	0.001	0.66	0.01
Log (northern spp.)	Log (area)	10	1.0	0.14	0.71	0.01
	Elevation	10	-1.4	0.001	0.70	0.01
	Communities	10	0.8	0.06	0.43	0.05
	Number of peaks	10	0.9	0.02	0.42	0.05
	Log (area)	8	0.9	0.20	0.75	0.005
	Elevation	8	-1.6	0.004	0.65	0.01
Log (endemics)	Communities	10	0.5	0.12	0.41	0.05
	Log (area)	8	0.8	0.40	0.60	0.05
Log (high elevation spp.)	Log (area)	10	1.4	0.14	0.78	0.001
	Elevation	10	-1.0	0.001	0.76	0.001
	Communities	10	1.1	0.07	0.49	0.05
	Number of peaks	10	1.3	0.02	0.44	0.05
	Log (area)	8	1.3	0.19	0.75	0.005
	Elevation	8	-1.1	0.003	0.65	0.01
Log (rare spp.)	Elevation	10	-4.8	0.003	0.55	0.05
	Log (area)	10	0.7	0.30	0.47	0.05
	Log (area)	8	0.48	0.49	0.58	0.05
	Elevation	8	-5.6	0.001	0.54	0.05
Log ( $S_1/P_1$ )	Number of peaks	10	-0.65	0.027	0.62	0.007
	Area	10	-0.65	0.009	0.62	0.007
	Elevation	10	-2.8	0.0004	0.49	0.025
	Communities	10	-8.6	0.075	0.47	0.03
	Log (area)	8	-0.72	0.28	0.69	0.01
	Area	8	-0.67	0.011	0.69	0.01
	Communities	8	-0.97	0.097	0.67	0.01
	Number of peaks	8	-0.67	0.027	0.67	0.01
Log ( $S_2/P_2$ )	Elevation	10	-2.7	0.0004	0.78	0.001
	Log (area)	10	-0.49	0.13	0.76	0.001
	Area	10	-0.55	0.0079	0.63	0.006
	Communities	10	-0.70	0.057	0.43	0.04
	Log (area)	8	-0.54	0.17	0.71	0.009
	Elevation	8	-2.8	0.0004	0.68	0.01
	Area	8	-0.51	0.007	0.58	0.03

size) and therefore we contrasted two data sets comprised of: (i) all ten areas (called below the 'larger' data set) and (ii) the eight largest areas (called below the 'smaller' data set). The unexpectedly higher richness of the two smallest areas was expressed in all floristic categories, but was most notable for total richness.

For the data set containing ten mountain ranges, area was the best predictor of two species richness categories (northern species and high elevation species), community

number was the best predictor of two species richness categories (total species and endemic species), and elevation was the best predictor of rare species richness (Table 1). For this data set, the number of peaks and area were equally good predictors of total species fraction, while elevation was the best predictor of high elevation species fraction.

For the data set containing eight mountain ranges, area was the best predictor for all richness variables ( $r^2=0.60-0.84$ ) and elevation usually ranked second ( $r^2=0.54-0.65$ ; Table 1). The smaller data set almost always had higher slope coefficients than the data set with ten mountain ranges (typically 30–300% higher) and higher coefficients of determination; this was most striking in the model predicting total species from log (area) (Table 1).

For the larger data set, four of the five significant log (species)–log (area) models had slope coefficients that were less than 0.14 (Table 1) and were thus ‘continental’ in the sense of MacArthur & Wilson (1967). The fifth significant model (the one for rare species) had a slope coefficient of 0.30, an ‘insular’ value. For the smaller data set, five of the seven significant log (species)–log (area) models had slope values above 0.20 (hence, ‘insular’), including the model for endemic species (0.40) and rare species (0.49). The consistent steepness of the rare species relationship is notable: rare species increased more quickly as area or elevation increased than did any other measure of richness.

Because of the relatively small number of data points in our analysis, we further examined our conclusion that the two smallest areas were outliers, by deleting all combinations of two data points from the full data set and repeating the regression analyses. We found that the only significant regressions ( $P < 0.05$ ) were ones that involved deletions of at least one of the two smallest areas. Furthermore, the independent variables in these significant regressions had the same relative importance for any given richness measure as they had for regressions based on the eight largest areas. The most significant models always involved deletion of both of the smallest areas. We concluded that the relationships exhibited by the eight largest areas are qualitatively different than those exhibited by the full data set.

### *Tests of model formulations*

Area and elevation were selected for more detailed analysis because they were the two most important predictors of species richness (Table 1). Total richness and high-elevation richness were used in this more thorough analysis because these were the largest richness categories. Four forms of the richness variables were used: richness, log (richness), species fraction and log (species fraction). Three topographic variables were used: area, log (area) and elevation.

For total species richness, ten of the twelve models were significant and untransformed area was the best predictor of this richness category (Table 2). The three best models ( $r^2=0.62-0.64$ ) included two linear models (species fraction–area and species–area) and one semi-log model [log (species fraction)–area]. For high elevation species richness, all twelve models were significant, with the coefficient of determination ranging from 0.73 to 0.78 for the ten best models. The greatest coefficient of determination was achieved for a log–log model, but several linear and semi-log models were only marginally lower in predictive strength. High-elevation species models accounted for a significantly higher percentage of the variation in species richness than did models of total species richness (Table 2). There was also a higher probability that these models were valid based on  $F$  statistics.

TABLE 2. A comparison of species–area and species–elevation models for the full data set (10 areas), using untransformed and log transformed data ( $b$  = intercept,  $m$  = slope coefficient).

Model	Dependent variable	Independent variable	$r^2$	$P > F$
Total richness				
$S_1/P_1 = b + mA$	Species fraction	Area	0.64	0.0058
$S_1 = b + mA$	Species	Area	0.64	0.0058
$\text{Log}(S_1/P_1) = b + mA$	Log species fraction	Area	0.62	0.007
$\text{Log } S_1 = b + mA$	Log species	Area	0.61	0.0074
$\text{Log}(S_1/P_1) = b + mE$	Log species fraction	Elevation	0.49	0.025
$\text{Log}(S_1/P_1) = b + mE$	Log species	Elevation	0.48	0.0267
$\text{Log}(S_1/P_1) = \text{Log } b + m \text{Log } A$	Log species fraction	Log area	0.41	0.05
$\text{Log } S_1 = \text{Log } b + m \text{Log } A$	Log species	Log area	0.40	0.0491
$S_1 = b + mE$	Species	Elevation	0.40	0.0497
$S_1/P_1 = b + mE$	Species fraction	Elevation	0.40	0.0497
$S_1 = b + m \text{Log } A$	Species	Log area	0.39	0.0528
$S_1/P_1 = b + m \text{Log } A$	Species fraction	Log area	0.39	0.0528
High elevation species				
$\text{Log } S_2 = \text{Log } b + m \text{Log } A$	Log species	Log area	0.78	0.0007
$\text{Log}(S_2/P_2) = b + mE$	Log species fraction	Elevation	0.78	0.0001
$S_2/P_2 = b + mA$	Species fraction	Area	0.77	0.0008
$S_2 = b + mA$	Species	Area	0.77	0.0008
$S_2/P_2 = b + mE$	Species fraction	Elevation	0.76	0.0011
$\text{Log } S_2 = b + mE$	Log species	Elevation	0.76	0.0011
$S_2 = b + m \text{Log } A$	Species	Log area	0.76	0.0011
$\text{Log}(S_2/P_2) = \text{Log } b + m \text{Log } A$	Log species fraction	Log area	0.76	0.001
$S_2/P_2 = b + mE$	Species fraction	Elevation	0.74	0.0015
$S_2 = b + mE$	Species	Elevation	0.73	0.0016
$\text{Log } S_2 = b + mA$	Log species	Area	0.65	0.0048
$\text{Log}(S_2/P_2) = b + mA$	Log species fraction	Area	0.63	0.006

### Multiple regressions

Multiple regression was performed to determine the relative variable contribution to the total model coefficient of determination. All possible combinations of uncorrelated independent variables were tested in models with total and high-elevation richness as the dependent variables.

Models with three independent variables explained about 30% more of the variance in total richness ( $r^2 = 0.62\text{--}0.89$ ) and about 12% more of the variance in high elevation richness ( $r^2 = 0.74\text{--}0.89$ ) than did single variable models. Elevation, number of peaks, and area always had positive coefficients in the models and latitude always had a negative coefficient. Isolation almost always (22 of 24 models) had a positive influence on richness, but explained only a small part of the variance in richness (0–6% in 21 models, 9–12% in three models). Number of peaks explained the greatest percentage of variance in total species richness. Area and elevation explained the greatest percentage of variance in high elevation species richness. The best multiple regression models (with the contribution of each variable to total  $r^2$  given in parentheses) were:

Total richness = Number of peaks (82%) – Latitude (5%) + Isolation (1%)  
(total  $r^2 = 0.89$ ;  $P > F$ , 0.003)

Total richness = Number of peaks (82%) – Latitude (5%) + Elevation (1%)  
(total  $r^2 = 0.88$ ;  $P > F$ , 0.003)

High elevation richness = Area (77%) + Isolation (6%) – Latitude (6%)  
 (total  $r^2 = 0.89$ ;  $P > F$ , 0.003)

High elevation richness = Elevation (73%) + Number of peaks (13%) + Isolation (2%)  
 (total  $r^2 = 0.88$ ;  $P > F$ , 0.004)

Because there are only ten mountain areas above 1680 m in our study area and the data set is thus relatively small, we tested the sensitivity of the multiple regression models to random deletions of single observations. All species-richness variables based on data sets of nine mountain ranges produced multiple regression models that were very similar to the models produced from the data set with ten mountain ranges, with only minor differences in the order of entry of the independent variables, the amount of variance each independent variable explained, the  $F$ -statistics for each independent variable, and the model coefficients for the independent variables (relative magnitude and sign). Based on this analysis, we concluded that our overall assessment of the importance and strength of the independent variables in predicting richness was not a function of small sample size.

#### *Correlation with area above 1830 m*

Six of the ten ranges surpass 1830 m, with the area available at this contour ranging from 1 to 30% of the area available at 1680 m (Appendix 1). Total and endemic richness were not correlated with area at this contour, but northern ( $R = 0.80$ ,  $P < 0.01$ ), high elevation ( $R = 0.70$ ,  $P < 0.05$ ), and rare species ( $R = 0.73$ ,  $P < 0.05$ ) richness were. These correlations were 10–25% lower than correlations using area above 1680 m.

## DISCUSSION

Our finding that measures of topographic and habitat diversity were as good as or better than area as predictors of richness is similar to that of Johnson (1975) for the avifauna of ten western North American mountain tops and that of Kitchener *et al.* (1980) for lizards of Australian nature reserves. The inappropriateness of the MacArthur & Wilson (1967) model for all vascular plants in these ten mountain ranges is further underscored by the weak and generally positive influence of isolation on richness. The lack of insularity is partly due to the lack of a sharp ecological contrast at the 1680 m contour (only 15–40% of the species were restricted to area above this contour; White, Miller & Ramseur 1984). Therefore, for a majority of the plant species present measurement of area and intermountain distance did not reflect total habitat area or ecological isolation.

The species–area relationship for restricted floristic groups was stronger than for total richness, and the slope coefficients for these floristic groups were higher than for total species richness and often fell within the range of insular slope values. Wyatt & Fowler (1977) obtained a similar result for endemic species on south-eastern U.S. granite outcrops, and Vuilleumier (1970) found that South American endemic birds were strongly correlated to mountain-top characteristics. These studies, together with our results, suggest that floristic groups with more restricted geographic distributions are characterized by steeper species–richness–environmental relationships.

No single model formulation was consistently predictively superior in this study. Total species richness was best modelled by linear equations. The magnitude of the coefficients of determination for high elevation species was not significantly affected by alternative combinations of independent variables in multiple regression models. The results are similar to the results of McNeill & Cody (1978) for vascular plants on St. Lawrence River

islands and the conclusions of Connor & McCoy (1979) on a wide range of published data sets.

We infer from these results that the equilibrium model of MacArthur & Wilson (1967) does not apply in our case. Immigration from the lower elevation species pool probably dominates over inter-mountain immigration. Furthermore, the source area of the present high elevation flora in the southern Appalachians is remote both in time and space. We believe that extinction, driven by climate change, has largely determined the species–area relationships we observed. Extinction of high elevation species was probably a function of maximum elevation and area available above critical contours. The steep species–area relationships for rare species, the importance of maximum elevation in predicting rare species richness, and the strong correlation between rare species richness and area above 1830 m together support this contention.

From results similar to ours, Brown (1971) inferred a non-equilibrium state for mammals of the Sierras, based in part on the influence of glacial and historic extinctions, and Billings (1977) noted that climatically driven fluctuation in available area for the alpine flora of the inter-mountain west was probably more important than contemporary area in predicting species richness. Only finer scale, process-level research on extinctions and immigrations (e.g. Riebesell 1982) can explain the causal factors behind our observations and confirm our interpretation.

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APPENDIX 1  
 The topographic, geographic, community and species richness characteristics of the southern Appalachians high peaks (adapted from White, Miller & Ramseur 1984)

Range	Area (km <sup>2</sup> ) > 1830 m	Area (km <sup>2</sup> ) > 1680 m	Number of peaks > 1680 m	Maximum elevation (m)	Isolation (km)	Number of community types	Number of species			Total richness (S <sub>1</sub> )	Species fraction S <sub>1</sub> /P <sub>1</sub>	Species fraction S <sub>2</sub> /P <sub>2</sub>
							Northern	Endemics	High elevation (S <sub>2</sub> )			
Great Smoky Mts	30.7	49.0	10	2024	6.1	8	18	26	44	18	0.54	0.63
Balsam Mts	28.2	29.4	20	1954	6.1	7	17	25	42	16	0.71	0.60
Black Mts	10.2	24.8	5	2037	3.3	3	18	16	34	15	0.35	0.49
Roan Mts	5.1	8.8	3	1916	23.9	5	14	18	32	13	0.28	0.46
Plott Balsams	10.2	5.7	1	1918	6.1	5	8	12	20	2	0.30	0.29
Craggies	2.6	2.0	1	1853	3.3	4	13	15	28	10	0.28	0.41
Grandfather Mts	0	1.1	1	1818	23.9	3	7	18	25	6	0.19	0.36
Mt. Rogers	0	0.4	3	1743	5.6	3	7	6	14	1	0.14	0.20
Mt. Pisgah	0	0.05	1	1743	7.8	2	6	10	16	7	0.34	0.23
Whitetop	0	0.03	1	1683	5.6	4	8	8	16	1	0.20	0.23

\* Fractions were computed as follows: S<sub>1</sub> = total richness for a particular mountain range; P<sub>1</sub> = total number of vascular plants in the whole data set (342 species); S<sub>2</sub> = number of high elevation species for a particular mountain range; P<sub>2</sub> = total number of high elevation species in the whole data set (seventy species).