A Quantitative Topographic Analysis of the Sky Islands: A Closer Examination of the Topography-Biodiversity Relationship in the Madrean Archipelago

David Coblentz
Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, NM

Kurt Riitters
Forest Health Monitoring, USDA Forest Service, Research Triangle Park, NC

***Abstract**—The relationship between topography and biodiversity is well documented in the Madrean Archipelago. However, despite this recognition, most biogeographical studies concerning the role of topography have relied primarily on a qualitative description of the landscape. Using an algorithm that operates on a high-resolution digital elevation model we present a quantitative analysis of the topographic fabric in the Madrean Archipelago and explored its utility by evaluating a topography-based predicted biodiversity map. In general, we find excellent agreement between the predicted and observed (based on land cover imagery) biodiversity throughout much of the Sky Island region. While readily acknowledging that many other biological factors influence biodiversity, this study establishes an important first-order estimate of the role topography plays in the regional- to continental-scale biodiversity, particularly in regions characterized by insular mountain fabrics such as the Sky Island region.*

Introduction

It is well known that many landscape characteristics (in particular, relief, slope, aspect, and gradient) play an important role in the distribution of vegetation and biodiversity (e.g., Brown 1978; Merriam 1890; Whittaker 1977; Whittaker and Niering 1965; among many others). For terrestrial habitats, variation in species diversity along gradients of elevation and available soil moisture are almost as striking as latitudinal variations (Cook 1969; Simpson 1964,). Just as the number of species decreases in progressively cooler climates as one moves from the tropics to the polar regions, so it also decreases in the cooler environments as one ascends mountains. This pattern has been well established for trees on mesic mountains of North America (Whittaker 1960, 1977).

The role of topography in the distribution of biodiversity in the arid regions of the Southwestern United States and Northern Mexico is particularly profound. In part, this is a consequence of the extreme aridity at the lower elevations that results in the greatest species diversity of most organisms at intermediate elevations in desert mountains (Whittaker and Niering 1965). In Southern Arizona, the oak woodland biome (at an elevation of about 1,500 m) defines a transition zone between the underlying tropical and overlying temperate life zones, and the ability of flora and fauna to mix across this elevation gradient is considered an important factor in the high level of biodiversity observed in the Sky Island region (Whittaker and Niering 1965; Brown and Lowe 1980; Felger and Wilson 1994; McLaughlin 1994).

Despite the important link between topography and biodiversity, studies of the relationship have been limited to a primarily *qualitative* framework. The current availability of high speed computing platforms, high-resolution digital elevation models, and land cover diversity data sets (e.g., Riitters et al. 2000), invites *quantitative* analyses and the testing of the relationships discussed in these previous investigations. Here, we undertake such a quantitative analysis by testing the hypothesis that a predictive biodiversity model based on a combination of topographic parameters (organization, roughness, gradient, and mean elevation) can explain the large-scale features of the observed regional biodiversity. We are particularly interested in the applicability of this predictive model in the Sky Island region where the mixing of floristic (Neotropic and Holarctic), faunal (the Neotropic and Nearctic) realms with three major climatic zones (tropical, subtropical, and temperate) is facilitated by high topographic relief and a strong N-S topographic grain orientation.

In the face of continuing global change, an understanding of the many factors affecting biodiversity is becoming increasing relevant. The approach presented here provides new ways of thinking about biodiversity and new assessment techniques to measure and assess it on a regional scale. We note at the onset that we are not proposing that high levels of biodiversity can be explained in terms of topography alone, but rather we seek to evaluate how much of the regional scale diversity is controlled by measurable aspects of the topographic fabric. Of particular interest is the evaluation of regions where large misfit exists between the predicted and observed biodiversity, which provides valuable information about the limitations of this approach.

Land Cover Diversity

Biodiversity is a popular concept that is often ill defined in terms of level of biological organization or spatial scale.

The use of land-cover diversity as a measure of biodiversity is justified by the observation that (at regional scales) community diversity is equivalent to biodiversity (Noss 1990; Stoms and Estes 1993; Wickham et al. 1995). While the existence of suitable land cover may not guarantee the existence of a species (the real object of biodiversity), the absence of suitable land cover usually precludes habitation, and furthermore a variety of land cover types may support a higher variety of species, at least in extra-tropical ecosystems. In this regard, we make the fundamental assumption that land cover diversity can be considered as a measure of potential species diversity.

The land cover diversity data set for the study area was created by using a pixel-based approach that computed a diversity index from the observed proportions of different land-cover types using information from the Global Land Cover Characterization (GLCC) project (Loveland et al. 2000). The maps have a nominal one-kilometer spatial resolution and were derived from satellite (AVHRR) imagery over the time period April 1992 to March 1993. The global thematic resolution is approximately 200 land-cover types, not all of which occur in the study area. We ignored water, urban, and agricultural pixels in order to focus on the diversity of semi-natural vegetation types.

In the present study, a 729 km^2 quadrat (27 x 27 pixels) was centered on each pixel of the original land-cover map, and a land-cover diversity index was calculated within the quadrat and stored in a new biodiversity map at the location of the subject pixel. Each pixel value on the biodiversity map thus represents the land-cover diversity within the surrounding blocks of the original data set. For simplicity, we used Simpson's index (Simpson 1949) that is usually calculated at the species level from the number of individuals of different species observed in a quadrat. In our application, it was calculated at the landscape level from the observed proportions (Pi) of the i different land-cover types in a quadrat as:

$$I = 1 - \Sigma \mathrm{P}i^2 \qquad (1)$$

The index I ranges from 0 to 1 with a larger index value indicating greater land-cover diversity.

The observed land cover diversity is shown in 2B. There are broad regions where the diversity reflects the regional topographic fabric (e.g., the Mogollon Rim, northern Rio Grande Rift, central Sierra Madre), and other areas where high diversity appears to be independent of topography (along the coastal plain of Sonora, Mexico, and along the Gila and Colorado Rivers). Histograms of the land cover diversity (LCD) for five subregions in the vicinity of the Sky Islands are shown in 3D of Coblentz (2004, this proceedings). In contrast to spatial distribution of the three principal topographic parameters (roughness, organization and fabric orientation—see figure 2 of Coblentz, this proceedings), the LCD distribution shows significantly less coherence within the individual provinces in the Sky Island region. This large degree of scatter (and associated skewing of all the distributions toward lower diversity) may reflect how the land-cover data were collected (especially the number of different land-cover types that were mapped) or our use of Simpson's index for the construction of the data set. We note that the use of other maps or indices could test these

possibilities. Relatively large variances within some provinces (e.g., the Rio Grande Rift and the Southern Basin and Range) could also indicate interactions between tectonic provinces and other drivers of land cover (e.g., water and history) that are not evenly distributed across the study area. We note that the Sierra Madre and Madrean Archipelago provinces have high mean values, relatively low standard deviations, and positive kurtosis (small distribution tails) substantiating the *a priori* observation that these two provinces are centers of high biodiversity.

Topographic Analysis

Landscape topography contains valuable information about the geodynamic, tectonic, and climatic history of a region. Important challenges remain, however, in the development of a quantitative framework for how to "read" this history from the observed topography. Clearly more useful information about topographic fabric is available to supplement basic statistical information. The approach we have taken is to use a 30-arc-second digital elevation model (providing a spatial resolution of about 1 km) to create a terrain classification data set based on information about the mean elevation, gradient, slope aspect, grain orientation, organization, and roughness using the synthetic slope organization method of Chapman (1952), which has been modified to take advantage of fast computing resources afforded by PCs (Guth 1987). Information about the topographic fabric of the Sky Island region using this method is discussed in Coblentz (2004, this proceedings) and Coblentz and Riitter (2004). Here, this information has been used to construct a predicted biodiversity map for the Sky Island region.

Predicted Biodiversity

Construction of a predicted biodiversity map based on the topographic information is based on our hypothesis that in many parts of the Southwest high levels of biodiversity correlate with topography exhibiting the following characteristics: (1) high roughness, (which leads to vertical stacking of biotic communities); (2) highly organized topographic grain oriented in the N-S direction (which encourages the mixture of flora and fauna between the tropic and temperate regions); (3) a median elevation of about 1,500 m (which maximizes mixing between tropical and temperature life zones within the vertically stacked biotic communities); and (4) a northward slope aspect (which effectively lowers the ecotone between the stacked biotic communities due to the cooler, moister environments on northward facing slopes). Following the principle of parsimony we have adopted a first-order approach that uses an unweighted sum of normalized values of these topographic quantities to construct a predicted biodiversity map for the study area.

In contrast to the topographic parameters, the spatial distribution of the land cover diversity shows significantly less coherence within the tectonic provinces. This large degree of scatter (and associated skewing of all the distributions toward lower diversity) may reflect how the land-cover data were collected (especially the number of different

land-cover types that were mapped) or our use of Simpson's index for the construction of the data set. We note that the use of other maps or indices could test these possibilities. Relatively large variances within some provinces (e.g., the Rio Grande Rift and the Southern Basin and Range) could also indicate interactions between tectonic provinces and other drivers of land cover (e.g., water and history) that are not evenly distributed across the study area. We note that the Sierra Madre and Madrean Archipelago provinces have high mean values, relatively low standard deviations, and positive kurtosis (small distribution tails) substantiating the *a priori* observation that these two provinces are centers of high biodiversity. If topographic and edaphic drivers are in fact the primary drivers of land cover diversity over the study area, these drivers may simply be less modified by other environmental factors in these provinces compared to other regions.

The resulting database (figure 1A) is renormalized and compared to the normalized observed Land Cover Diversity database (figure 1B). The spatial variations in the misfit between the predicted and observed biodiversity datasets is shown in figure 1C, with regions of positive and negative misfit corresponding to over- and under-predicted biodiversity, respectively. Comparison of the misfit between the calculated and observed biodiversity distributions within the five provinces is facilitated by histograms of the misfit (figure 1D).

High levels of biodiversity are predicted along the western margin of the Sierra Madre (where canyon incisement is greatest), throughout much of the Madrean Archipelago, the Grand Canyon region of the Colorado Plateau, and in the central Rio Grande Rift. In contrast, much of the Southern Basin and Range, Baja California, and coastal Sonora are characterized by low predicted biodiversity values. Examination of the misfit plot (figure 1C) shows good agreement between the predicted and observed biodiversity throughout much of the Sierra Madre and Madrean Archipelago provinces. Our model overestimates the biodiversity throughout much of the central Colorado Plateau, the eastern Sky Island region south in New Mexico, the southern Rio Grande Rift, and the Chihauhuan Desert region east of the Sierra Madre highlands. In contrast, our model underestimates the biodiversity in large regions of the Sonoran coastal plain, along the Gila River in western Arizona, and in the Salton Trough of southern California where other factors contributing to elevated land cover diversity values (namely agricultural development) have not been taken into account.

The misfit distributions for the individual provinces are shown in figure 1D. The misfit in the Sierra Madre is remarkably Gaussian with a mean value very close to zero. The misfit for the other provinces tend to be skewed to positive (overestimation) misfit values. With the exception of the Rio Grande Rift (which samples both large regions of over- and underestimation in the southern and northern sections of the rift, respectively), the individual provinces show very low kurtosis values, indicating a sharp peak in the distribution about the mean (particularly for the Madrean Archipelago and Southern Basin and Range provinces which have kurtosis values less than 0.1). We note, however, that only a weak linear correlation exists between the calculated and observed values for the province-wide distributions (R-squared values less

than 0.15 for the Sierra Madre and Southern Basin and Range provinces and near-zero values for the other three provinces). This may be the result of a non-linear relationship between the predicted and observed values (which might be expected given the first-order nature of our predictive algorithm) or may reflect that fact that spatially each of the provinces have larges regions of poor correlation between prediction and observation that prevents the establishment of high R-squared values for province-wide distributions.

Discussion

From biological perspective, topographic variables are indirect factors, which do not necessarily have a physiological influence on species (in contrast to direct factors such as temperature and soil nutrients.) However, while the use of direct factors is preferable for predicting biodiversity, data may not be available, particularly for large regions and inaccessible areas. We are therefore motivated to explore the applicability of predicting biodiversity based on topographic parameters that are readily measured. In the Southwest, the spatial distribution of topography plays an important role in the distribution of biodiversity, particularly in areas characterized by insular mountain ranges. The large elevation gradients in this region have resulted in stacked biotic communities in which species with broadly similar climatic preferences sort themselves along the elevational gradient where the blend of temperature and aridity best supports them. Species of plants and animals originating in north temperate areas are found at the higher elevations, while species from the more tropical south occur nearer the base (Whittaker and Niering 1965, 1968; Brown and Lowe 1980). On a local scale, topography facilitates the compression of biotic communities into relatively constricted vertical spaces and produces rapid species turnover (McLaughlin 1994), and encourages the mingling of species that would normally be widely separated (Felger and Wilson 1994). This is quantifiable in terms of the topographic roughness that we find to be significantly higher in the Madrean Archipelago province relative to the surrounding areas. This aspect of the topography combined with the regional-scale NW-SE orientation of the topographic grain in the Sierra Madre and Madrean Archipelago provinces (that encourages the movement of floral and faunal species up from the neotropical into the temperate biotic zone) are the two most important geographic factors contributing to the high biodiversity in the Madrean Archipelago province.

We readily acknowledge that a predictive biodiversity model based solely on topographic parameters is an over simplification. The principal purpose of the analysis present above is to demonstrate the utility of performing a quantitative topographic analysis and evaluate to what degree topography controls the biodiversity in this region. Other contributing factors that have not been taken into account in our model include information about the bimodal rainfall pattern related to the Mexican Monsoon, the highly diverse bedrock geology of the region, hydrologic distribution, and other topographic parameters such as the slope aspect. Incorporation of these additional factors will need to wait until comprehensive regional-scale
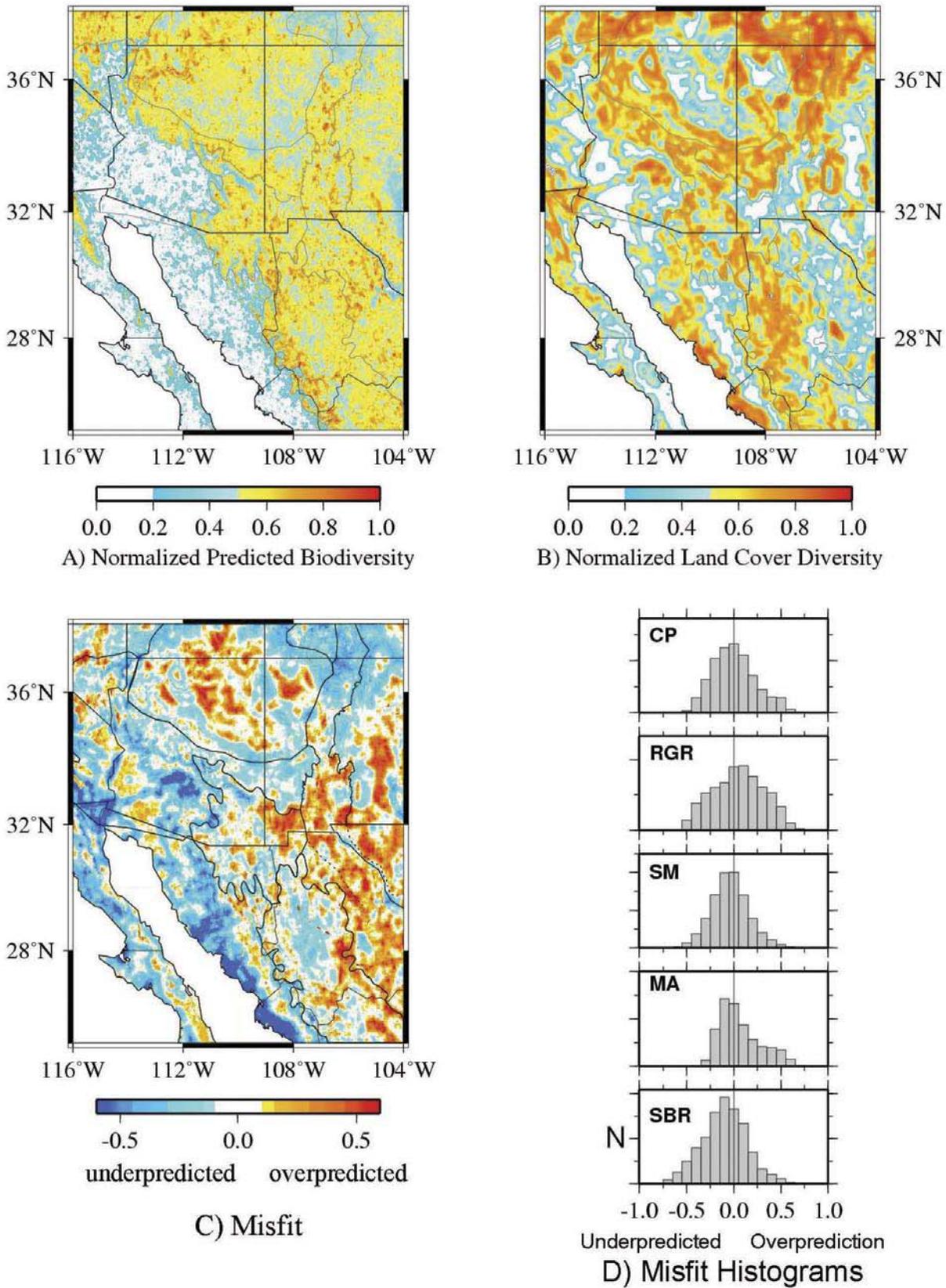
Figure 1—(A) Predicted biodiversity based on the topographic analysis algorithm discussed in the text. **(B)** Normalized observed biodiversity based on the land cover diversity data set. Dark and light colors designate regions of low and high land cover diversity, respectively. Simpson's (1949) index of diversity was computed for each 1 km^2 location from a map of seasonal land cover regions (Loveland et al. 1995, 2000) by using the proportions of different land cover types in the surrounding 27 km x 27 km quadrat. Water, urban and agricultural land cover types were not included in the diversity index calculation. **(C)** Misfit values of the difference between the predicted and observed data sets. Red and blue regions designate regions where the biodiversity has been over- and under-predicted, respectively. **(D)** Histograms of the misfit for the five topographic provinces.

databases are available. We note that in the Southwest the role of soil diversity can be expected to have a profound effect on the biodiversity given the complex geologic history that has resulted in the superimposition of sequences of pre-Cambrian igneous, Paleozoic sedimentary, and Mesozoic volcanic rocks, each of which has a particular soil-vegetation affinity.

While we have only considered the role played by topography in the present-day distribution of biodiversity, we note that its effect becomes even more pronounced over timescales long enough to take climatic change into account. In particular, over the past two million years the location and mix of species along the altitudinal gradients has changed, as cycles of glaciation and warming have triggered species migrations up, down, or off mountain ranges (Van Devender 1990). During cooler times, which have predominated, woodland flora and fauna populated the valleys separating the mountain ranges and formerly isolated species would mix. Northern temperate species immigrated into the region from the north while many desert species would retreat southward. During warmer interglacials, such as the present, subtropical desert vegetation returned. Woodland vegetation would migrate upslope and become stranded on individual ranges, as the valleys between the mountain ranges became barriers they could not penetrate. Thus, quantitative topographic analyses such as those presented in this study can make a significant contribution to studies of the relationship between biodiversity and climatic change (Nobel 1993; Allen and Breshears 1998). Furthermore, the method and results presented above demonstrate that this approach could lead to an adjustment for topography to be used to facilitate a comparison between the biodiversity of two areas by providing a way to remove the potential effects of long-termed constant factors (such as topography) thereby increasing the sensitivity of studies of shorter termed factors such as climate or biotic variables.

From a more speculative perspective, several researchers have recently investigated the implications of characteristic scaling lengths in biology (e.g., Gardener et al. 1987; Wiens and Milne 1989; Milne 1991; Levin, 1992; Allen et al. 1999; Siemann and Brown 1999; Allen and Holling 2002). If they indeed exist, then corresponding characteristic topographic scales must surely play an important role. The approach presented in the present study provides a foundation to test this hypothesis by comparing the characteristic scales of the biodiversity/topography relationship with those being evaluated within a biology/ecology framework. Demonstration of a positive correlation would support arguments that large area patterns in both topography and ecology are the result of long-term tectonic processes; suggesting that continental-scale biodiversity should be studied in the context of large-scale physical processes such as topographic evolution in response to plate tectonic forces as opposed to local-scale phenomena.

Conclusions

In this study we have tested the hypothesis that a combination of three measurable topographic quantities (organization, roughness, and mean elevation) can be used to assemble a reasonable predictive map of spatial biodiversity. Within the underlying assumptions discussed above, we draw the following conclusions: (1) A quantitative topographic analysis is a valuable tool for understanding the distribution of biodiversity, particularly in regions where insular mountain ranges dominate the topographic distribution. Histograms of the misfit between the calculated and predicted biodiversity make a strong case for good general agreement between the datasets. (2) The predicted biodiversity is overestimated in many regions lacking significant vertical relief (e.g., the central Colorado Plateau, Rio Grande Rift, and the low desert areas of the Southern Basin and Range). (3) In regions where topography is expected to play an important role in the high levels of biodiversity (e.g., Madrean Archipelago and Sierra Madre provinces) we find a good correlation between our predicted biodiversity model and observation. (4) The results presented in this study make an important contribution to efforts aimed at establishing predictive geoecological models for describing areal biotic distributions. As such, we feel our results are a significant improvement over efforts seeking correlations in land cover maps. We note that good predictions were only obtained for regions with particular topographic characteristics.

Acknowledgments

References

Allen, C. D.; Breshears, D. D. 1998. Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. Proceedings of the National Academy of Sciences. 95:14839-14842.

Allen, C. R.; Forys, E. A.; Holling, C. S. 1999. Body mass patterns predict invasions and extinctions in transforming landscapes. Ecosystems. 2:114-121.

Allen, C. R.; Holling, C. S. 2002. Cross-scale structure and scale breaks in ecosystems and other complex systems. Ecosystems: 5:315-318.

Brown, D. E.; Lowe, C. H. 1980. Biotic communities of the Southwest. USDA Forest Service General Technical Report RM-78.

Brown, J. H. 1978. The theory of insular biogeography and the distributions of boreal birds and mammals. Great Basin Naturalist Memoirs. 2:209-227.

Chapman, C. A. 1952. A new quantitative method of topographic analysis. American Journal of Science. 250:428-452.

Coblentz, D. 2004. Tectonic evolution of the Madrean Archipelago and its impact on the geoecology of the Sky Islands, this proceedings.

Coblentz, D.; Riitter, K. 2004. Topographic controls on the regional-scale biodiversity of the Southwestern U.S., in press, Journal of Biogeography.

Cook, R. E. 1969. Variation in species density of North American birds. Systematic Zoology. 18:63-84.

Felger, R. S.; Wilson, M. F. 1994. Northern Sierra Madre Occidental and its Apachian outliers: a neglected center of biodiversity. In: F. Leonard DeBano; Peter F. Ffolliott; Alfredo Ortega-Rubio; Gerald J. Gottfried; Robert H. Hamre; Carleton B. Edminster,

tech. coords. Biodiversity and management of the Madrean Archipelago: the Sky Islands of Southwestern United States and Northwestern Mexico. Sept. 19-23 1994. Tucson, AZ: Gen. Tech. Rep. RM-GTR-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 36-59.

Gardner, R. H.; Milne, B. T.; Turner, M. G.; O'Neill, R.V. 1987. Neutral models for the analysis of broad-scale landscape pattern. Landscape Ecology. 1:19-28.

Guth, P.L.; Ressler, E. K.; Bacastow, T. S. 1987. Microcomputer program for manipulating large digital terrain models. Computers and Geosciences. 13:209-213.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology. 73:1942-1968.

Loveland, T. R.; Reed, B. C.; Brown, J. F.; Ohlen, D. O.; Zhu, J.; Yang, L.; Merchant, J. W. 2000. Development of a global land cover characteristics database and IGBP DISCover from 1-km AVHRR data. International Journal of Remote Sensing. 21:1303-1330.

McLaughlin, S. 1994. An overview of the flora of the Sky Islands, southeastern Arizona: diversity, affinities, andiInsularity. In: F. Leonard DeBano; Peter F. Ffolliott; Alfredo Ortega-Rubio; Gerald J. Gottfried; Robert H. Hamre; Carleton B. Edminster, tech. coords. Biodiversity and management of the Madrean Archipelago: the Sky Islands of Southwestern United States and Northwestern Mexico. Sept. 19-23 1994. Tucson, AZ: Gen. Tech. Rep. RM-GTR-264. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 60-70.

Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and the desert of the Little Colorado, Arizona. North American Fauna. 3:1-136.

Milne, B. T. 1991. Lessons from applying fractal models to landscape patterns. In: Quantitative methods in landscape ecology. M. G. Turner; R. H. Gardner, eds. Springer-Verlag, New York: 199-235.

Noble, I. R. 1993. A model of the responses of ecotones to climate changes. Ecological Applications. 3:396-403

Noss, R. F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. Conservation Biology. 4:355-364.

Peet, R. K. 1974. The measurement of species diversity. Annual Reviews of Ecology and Systematics. 5:285-307.

Riitters, K. H.; Wickham, J. D.; Vogelmann, J. E.; Jones, K. B. 2000. National land-cover pattern data. Ecology. 81:604-604.

Siemann, E.; Brown, J. H. 1999. Gaps in mammalian size distributions reexamined. Ecology. 80:2788-2792.

Simpson, E. H. 1949. Measurement of diversity. Nature. 163:688.

Simpson, G. G. 1964. Species density of North America mammals. Systematic Zoology. 13:57-73.

Stoms, D. M.; Estes, J. E. 1993. A remote sensing research agenda for mapping and monitoring biodiversity. International Journal of Remote Sensing. 14:1839-1860.

Van Devender, T. R. 1990. Late Quaternary vegetation and climate of the Sonoran Desert, United States and Mexico. In: J. L. Betancourt; T. R. Van Devender; P. S. Martin, eds. Packrat middens: The last 40,000 years of biotic change. The University of Arizona Press, Tucson: 134-164.

Wickham, J. D.; Wade, T. G.; Jones, K. B; O'Neill, R. V.; Riitters, K. H. 1995. Diversity of ecological communities of the United States. Vegetation. 119:91-100.

Wiens, J. A.; Milne, B. T. 1989. Scaling of 'landscapes' in landscape ecology, or, landscape ecology from a beetle's perspective. Landscape Ecology. 3:87-96

Wessel, P.; Smith, W. H. F. 1991. Free software helps map and display data. EOS Transactions of the American Geophysical Society. 72, 441.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecology Monographs. 30:279-338.

Whittaker, R. H. 1977. Evolution of species diversity in land communities, In: M. K. Hect; W. C. Steere; B Wallace, eds. Evolutionary Biology. 10. Plenum Press, New York: 1-67.

Whittaker, R. H.; Niering, W. A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Journal of Ecology. 46:429-452.