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ORIGINAL ARTICLE

Topographic controls on the regional-scale biodiversity of the south-western USA

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ABSTRACT

Aim Topography is a fundamental geophysical observable that contains valuable information about the geodynamic, tectonic and climatic history of a region. Here, we extend the traditional uses of topographic analysis to evaluate the role played by topography in the distribution of regional-scale biodiversity in the south-western USA. An important aspect of our study is its ability to provide a way to quantify characteristics of the topographic fabric and to construct predictive models that can be used to test hypotheses that relate topography and biodiversity.

Location South-western USA region of the North American Cordillera.

Methods Our approach begins with a quantitative analysis of the topography and the construction of a predicted biodiversity map based on measurable topographic quantities: organization, roughness, slope aspect, grain orientation and mean elevation. We then make a quantitative comparison between the predicted and observed biodiversity, based on the assumption that land-cover diversity is a plausible measure of regional-scale biodiversity. Land-cover information used for this study was collected as part of the U.S.G.S. global land cover characteristics (GLCC) project and is derived from satellite (AVHRR) imagery.

Results To a first order, the predicted regional-scale biodiversity based on our topographic model shows a good correlation with the observed biodiversity (as estimated from the land-cover diversity). Our model overestimates the biodiversity in many parts of the Colorado Plateau, Rio Grande Rift, and the low desert regions of the Southern Basin and Range, suggesting that in these provinces a biodiversity estimate based solely on topography is an over-simplification. However, much of the Madrean Archipelago and Sierra Madre provinces, which are centres of high biodiversity in this region, show excellent agreement between the observed and predicted biodiversity.

Main conclusions While we acknowledge that many other factors in addition to topography have an important influence on biodiversity (particularly on a local scale), we conclude that topography plays a primary role in the regional to continental-scale biodiversity, particularly in regions characterized by insular mountain fabrics.

Keywords

Geoecology, landscape ecology, topographic analysis, land-cover diversity, biodiversity, spatial patterns, tectonics.

INTRODUCTION

Many topographic characteristics of the landscape (e.g. relief, slope, aspect, gradient, slope curvature, slope length and contour curvature) play important roles in the distribution of vegetation and biodiversity (e.g. Merriam, 1890, 1894; Whittaker & Niering, 1965, 1968; Vuilleumier, 1970; Brown, 1971, 1978; Hastings *et al.*, 1972; Simpson, 1975; Hanawalt & Whittaker, 1976; Whittaker, 1977; Behle, 1978; Johnson, 1978; Peet, 1978; Patterson, 1980; Cole, 1982; Allen & Peet, 1990; Allen *et al.*, 1991; Huggett, 1995; Burke, 1999; Hansen & Rotella, 1999). For terrestrial habitats, variation in species diversity along gradients of elevation and available soil moisture are almost as striking as latitudinal variations, which are well recognized (Simpson, 1964; Cook, 1969). Just as the number of species decreases in progressively cooler climates as one moves from tropical to 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 south-western US and northern Mexico is particularly profound. In desert regions, the extreme aridity of the lower elevations offsets this general trend in diversity and in desert mountains species diversity of most organisms is thought to be greatest at intermediate elevations (e.g. Whittaker & Niering, 1965). A diagrammatic profile of a hypothetical mountain in southern Arizona showing the vertical climatic zonation and concordance of biotic communities (Fig. 1) illustrates that the oak woodland biome (at an elevation of *c.* 1500 m) defines a transition zone between the underlying tropical and overlying temperate life zones. 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 this region (Whittaker & Niering, 1965, 1968; Brown & Lowe, 1980; Felger & Wilson, 1994; McLaughlin, 1994).

Despite the important link between topography and biodiversity, studies of the relationship have been limited to a primarily *qualitative* framework (see e.g. several discussions in Brown & Gibson, 1983). The current availability of high-speed computing platforms, high-resolution digital elevation models (DEM) (e.g. 30 arcsec or *c.* 1 km resolution) and land-cover diversity data sets (e.g. Riitters *et al.*, 2000), invites quantitative analyses to test the relationships discussed in these previous investigations.

In the present study, we undertake such a quantitative analysis by testing the hypothesis that a predictive biodiversity model based on a combination of topographic parameters (specifically topographic organization, roughness, gradient and mean elevation) can explain the large-scale features of the observed regional biodiversity. We have selected the south-western US as a study area for two primary reasons: first, the association between high habitat diversity and the high level of topographic relief in this region has long been recognized (e.g. Simpson, 1964; Cook, 1969; McCoy & Connor, 1980; Brown & Gibson, 1983) and secondly, the Madrean Archipelago (centrally located in the study area) ranks as one of the three top mega-diversity centres of the world (Felger & Wilson, 1994; Warshall, 1994). A primary control on the biodiversity of this region is the mixing of two major floristic zones (Neotropic and Holarctic), two major faunal realms (the Neotropic and Nearctic), and three major climatic zones (tropical, subtropical and temperate). This mixing is facilitated by the high topographic relief and strong N–S orientation of the topographic grain and we are motivated to quantitatively evaluate the role topography plays in the regional-scale distribution of biodiversity.

We begin with a description of the physiographical features of the south-west followed by a discussion of how the various stages in the tectonic evolution of the western US helped create the present-day topography. We test this hypothesis by comparing a predicted biodiversity map constructed from a combination of these physiographical quantities with an observed land-cover diversity data set.

In the face of continuing global change, an understanding of the many factors affecting biodiversity is becoming increasingly 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 the measurable aspects of the topographic fabric.

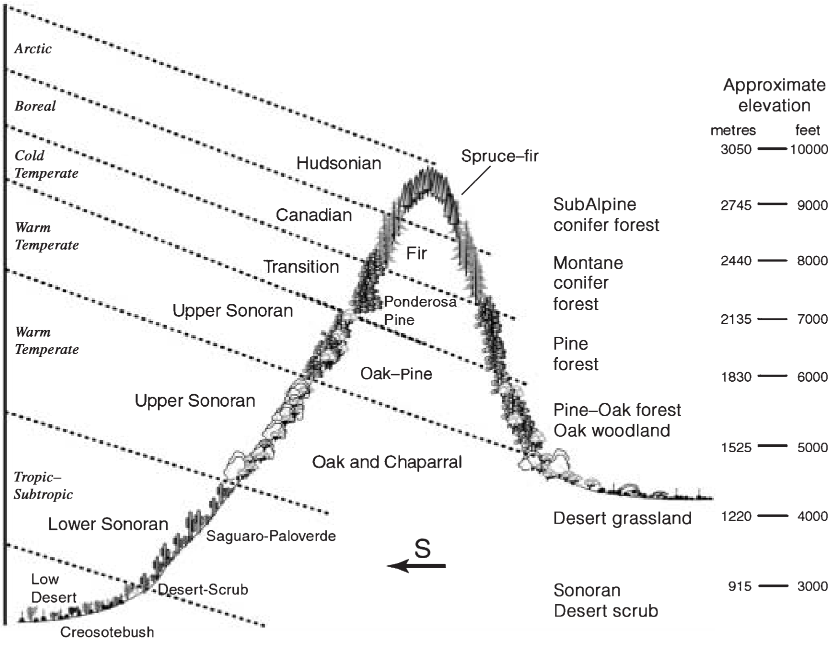

Figure 1 Diagrammatic profile of a hypothetical mountain in southern Arizona indicating the vertical climatic zonation and concordance of biotic communities (after Brown, 1982).

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.

TECTONIC EVOLUTION OF THE SOUTH-WEST

The present-day topography of the western US is inexorably coupled to the complex tectonic history of the North American Cordillera. The Cordillera, a mountain belt extending from Alaska to Guatemala, was formed by the interaction of the Pacific, North American, Farallon and Juan de Fuca plates over the past several hundred million years. Most of the observable topographic features in this region are the result of continental deformation during the final two tectonic stages: the predominately compressional events associated with Cretaceous to early Cenozoic (*c.* 200–60 Ma) subduction off western North America, and more recent extensional tectonic events which remain ongoing in many parts of the western US.

Most of the Cretaceous and the early Tertiary subduction of the Farallon plate beneath North American produced widespread compressional tectonics throughout most of the region. As this subduction evolved, a zone of deformation propagated eastward producing 'thin-skinned' deformation (often referred to as the Sevier Orogeny) where the lithosphere was sufficiently weak. The characteristic style of this deformation phase was folding and thrusting of Palaeozoic and Mesozoic sedimentary rocks from west to east along steep westward dipping thrust faults. The Sevier thrust faulting formed a large mountain system of north–south trending topography that has subsequently collapsed due to the weakness of the lithosphere in this region. Some Sevier topographic features are preserved in the faulted Basin and Range sequences as well as along the western margin of the Uinta and Wind River Mountains. As the deformation progressed further east during the Late Cretaceous and Early Cenozoic (*c.* 60 Ma) into stronger parts of the North American plate, deeper parts of the crust become involved (often referred to as the Laramide Orogeny). Mountain ranges formed during this deformational phase include the Rocky Mountains, the San Juans, the Gore Range and the Sawatch Range in Colorado; the Sangre de Cristos and Sandias in New Mexico; the Uintas and Wasatch Range in Utah; the Black Hills in South Dakota; the Bitterroot Range in Montana and Idaho; the Bighorns and Wind River Range in Wyoming; and the Franklin Mountains of West Texas. This topography is characterized by uplifted blocks of crust that include Phanerozoic sedimentary rocks as well as the underlying Precambrian igneous and metamorphic rocks that make up the core or basement of the continental crust.

Starting *c.* 30 Ma the elevated topography of the cordillera began to collapse in response to a transition from compression-dominated subduction of the Farallon plate off the western coast of North America to transcurrent motion between the Pacific and North American plates. Extensional tectonics produced by this gravitational collapse is responsible for the dominant present-day topographic fabric of *en echelon* north–south oriented mountain ranges separated by valleys filled with erosional detritus. Extensional processes during this period also formed the several large mountain ranges including the Tetons in Wyoming and the Sierra Nevada in California.

PRESENT-DAY PHYSIOGRAPHY OF THE SOUTH-WEST

This historic tectonic activity has formed the present-day high-standing landmass of the south-western US that can be divided into five primary provinces: The Basin and Range, the Colorado Plateau, the Rio Grande Rift, the Northern Sierra Madre Occidental and the Madrean Archipelago. The Basin and Range, characterized by its disrupted crust, lies to the west and south of the relatively coherent Colorado Plateau. The Rio Grande Rift is a region of modest extension to the east and south of the Colorado Plateau. West of the rift lies the complex topographic assemblage of the Madrean Archipelago, south of which is the volcanic plateau of the Sierra Madre. Each of these provinces is readily distinguishable in a topographic map of the region (Fig. 2). A brief description of each of the provinces follows.

The Colorado Plateau (Fig. 2, region A) is enigmatic in that it has apparently remained a relatively rigid and undeformed during the tectonic activities that deformed its neighbouring provinces. While the plateau has significant topographic range (*c.* 3500 m) and high mean elevation (*c.* 1899 m), the distribution of elevations has a relatively low standard deviation (346 m) indicative of a small deviation from the average value. Furthermore, low skewness (0.1) and kurtosis (0.7) values reflect a near-Gaussian elevation distribution.

The Rio Grande Rift (Fig. 2, region B) stands out on a regional topographic map as a 1000-km long rift system that separates the Colorado Plateau and the Basin and Range provinces from the Great Plains. The rift is characterized by broad flat lying topography along the rift axis, bounded by sharp escarpments (e.g. the Sangre de Cristos, Sandias, Manzanos and Sacramento). The topographic distribution of the rift is unique among the provinces for marked non-Gaussian distribution. Because the rift samples two elevation populations (the flat-lying rift valley floor characterized by relatively low elevation and little relief, and the elevation rift margins characterized by steep topographic escarpments and large vertical relief), the distribution is bimodal. As a consequence, the rift is characterized by a large positive skewness value (0.7) – indicative of an extended distribution 'tail' towards higher elevations, and a large negative kurtosis (−0.5) –indicative of a *platykurtic* distribution which is also reflected in the large standard deviation (491 m).

The Sierra Madre Occidental (Fig. 2, region C) is a large volcanic plateau in western Mexico extending parallel to the Pacific coastline for more that 1200 km from the US–Mexico border (31° N) to the Trans-Mexican Volcanic Belt (21° N). The topography of the northern Sierra Madre is characterized by high average elevation (1909 m) and large topographic

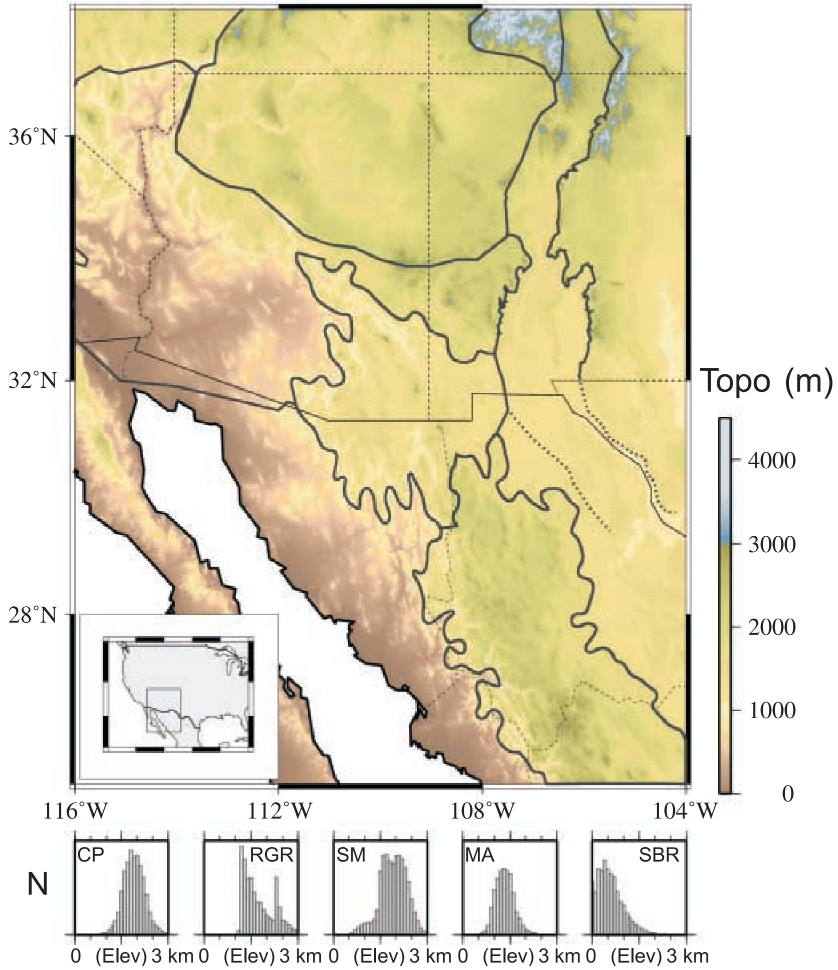

Figure 2 (a) Topography of the south-western US. The five major tectonic provinces are indicated with letters: A, Colorado Plateau; B, Rio Grande Rift; C, Sierra Madre Occidental; D, Madrean Archipelago; E, Southern Basin and Range. (b) Histograms of the topographic distribution for the five tectonic provinces of the south-west as shown in Fig. 1. The histogram populations are based on a sampling of the topography data set at a 30-arcsec resolution (*c.* 1 km). Values for the mean, standard deviation, skewness and kurtosis are listed in Table 1.

range (2811 m). In contrast to the other provinces, the topographic relief of the Sierra Madre is not the product of elevated mountain ranges, but rather incised canyons (e.g. the Barranca de Cobre). In many respects this topography can be thought of as ‘negative’ in the sense that the relief is downward as opposed to upward as in the neighbouring provinces. The western edge is quite steep while the eastern topographic gradients from the Sierra Madre into the central Mexican Plateau are relatively small. The elevation distribution is fairly flat about the mean value (yielding a small kurtosis value of 0.1), shows a skewness to lower elevation values (−0.4) reflecting a sampling of lower elevations along the coastal plain of Sonora, and has a fairly large standard deviation (428 m). The regional fabric of the Sierra Madre is aligned in a NW–SE orientation and is thought to form an important corridor of dispersal for tropical flora and fauna moving in response to climatic change (Felger & Wilson, 1994).

The Madrean Archipelago (Fig. 2, region D) spans the region formed by the common borders of Arizona, New Mexico, and the northern Mexican states of Sonora and Chihuahua. The term ‘archipelago’ (defined as a chain or group of islands) metaphorically reflects the insular nature of the roughly 40 isolated mountain ranges in this region (Warshall, 1994). This province is also referred to as the sky islands region, as the isolated mountain ranges (islands) are surrounded by intervening valleys of grassland and desert (sea) which acts as barriers to the movement of woodland and forest species (Heald, 1967; McLaughlin, 1994; Warshall, 1994). Biogeographically, this region forces an important biological bridge between the Colorado Plateau and Rocky Mountains to the north and the Sierra Madre Occidentals and their corresponding plateaus in the south. The topography of the Madrean Archipelago is characterized by isolated mountain ranges elongated in a NW–SE direction. There are many area of locally very large vertical relief (more than 2000 m across the Santa Catalina and Pinaleno Mountains), but the topographic range (2057 m), mean elevation (1331 m) and standard deviations (292 m) are all relatively small compared with the neighbouring provinces. A significant amount of high elevation associated with the high peaks of the ‘sky islands’ results in a high skewness value (0.5) with the distribution tail towards high elevations.

The Southern Basin and Range Province (Fig. 2, region E) is the best example of topography formed in response to the ongoing extension in the south-west. The region has been stretched and extended as much as 100% since the early Tertiary and has produced NW–SE oriented isolated mountain ranges. While elevations in this province approach 3400 m

Table 1 Statistical values for the five tectonic provinces

Province	Average	Standard deviation	Skewness	Kurtosis	Minimum	Maximum
Elevation						
CP	1903	349	0.10	0.68	481	3387
RGR	1605	471	1.07	0.40	783	3464
SM	1564	690	−0.12	−1.18	128	3005
MA	1316	288	0.24	0.79	551	2508
SBR	1018	623	0.34	−0.54	0	3221
Orientation*						
CP	−1.2	28.3	−0.14	−0.36	−88.4	75.6
RGR	−8.8	11.5	0.29	0.60	−83.5	60.9
SM	−10.9	17.4	1.01	1.82	−65.2	69.3
MA	−18.8	23.4	0.26	0.55	−82.5	71.3
SBR	−12.5	27.5	0.41	0.10	−83.5	84.9
Organization						
CP	0.79	0.36	1.19	2.70	0.06	3.37
RGR	1.07	0.57	1.18	1.78	0.04	4.31
SM	0.69	0.32	1.21	3.00	0.04	3.26
MA	0.92	0.53	1.39	2.31	0.08	4.23
SBR	0.92	0.50	1.44	3.03	0.04	4.86
Roughness						
CP	0.18	0.06	1.90	5.55	0.09	0.61
RGR	0.16	0.05	0.63	−0.27	0.07	0.34
SM	0.26	0.07	0.92	1.30	0.09	0.62
MA	0.18	0.05	0.49	−0.29	0.07	0.39
SBR	0.18	0.05	0.37	−0.10	0.06	0.42
Land-cover diversity						
CP	138.3	53.6	−0.59	−0.18	0.0	236.0
RGR	128.7	60.2	−0.21	−0.80	−0.4	233.8
SM	137.6	44.6	−0.93	0.32	−0.4	230.3
MA	137.9	45.2	−0.83	0.16	−0.4	212.5
SBR	122.2	57.7	−0.61	−0.71	−0.4	239.2
Misfit						
CP	0.00	0.23	0.41	−0.21	−0.65	0.89
RGR	0.05	0.27	0.00	−0.72	−0.60	0.91
SM	−0.04	0.20	0.22	0.18	−0.64	0.84
MA	−0.02	0.22	0.08	0.12	−0.70	0.89
SBR	−0.10	0.24	0.00	0.00	−0.84	0.89

CP, Colorado Plateau; RGR, Rio Grande Rift; SM, Sierra Madre Occidental; MA, Madrean Archipelago; SBR, Southern Basin and Range.
*Measured in degrees east of north.

(e.g. in the Spring Mountains near Las Vegas), the average elevation of the province is relatively low (333 m) with many parts slightly above or below sea level (e.g. in the Salton Trough of Southern California). The distribution of elevations is non-Gaussian with high values of both the skewness (1.1) and kurtosis (1.8), reflecting large tails in the distribution.

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 scale, community diversity is equivalent to biodiversity (Noss, 1990; Stoms & Estes, 1993; Wickham *et al.*, 1995). In Noss' (1990) conceptual model of a biodiversity hierarchy, an index of land-cover diversity describes the regional-compositional aspect of biodiversity, and our measurement scale (729 km^2) is appropriate for characterizing the regional diversity of biomes in the south-western US (Gosz & Sharpe, 1989). 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, land-cover diversity can be considered as a measure of potential species

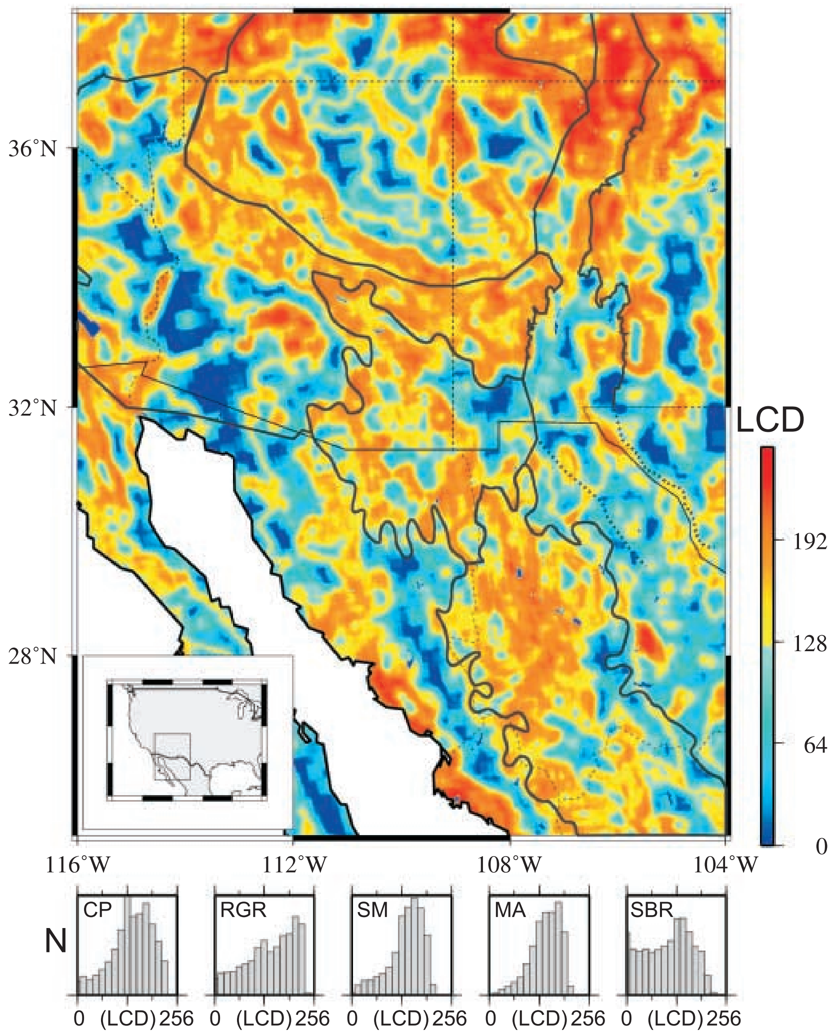

Figure 3 (a) Land-cover diversity for the south-western US Simpson's (1949) index of diversity was computed for each 1 km^2 location from a map of seasonal land-cover regions (Loveland *et al.*, 1995, 2000) by using the proportions of different land-cover types in the surrounding 27 km × 27 km quadrat. Water, urban and agricultural land-cover types were not included in the diversity index calculation. (b) Histograms of the land-cover diversity distribution for the five tectonic provinces as shown in Fig. 1.

diversity. In any case, knowing the spatial distribution of land-cover diversity and where diversification is more or less associated with topography provides insights into regional-scale patterns of biodiversity. Using a similar land-cover map at continental scale, Wickham *et al.* (1995) found that the relationship between land-cover richness (number of land-cover types in the window) and elevation range (difference between maximum and minimum elevation) resembled typical species–area curves with an asymptote for a window size of *c.* 12,000 square miles. Their analysis highlighted the sharp west-to-east decrease in richness at continental scale and was relatively insensitive to gradients within the south-western US where much smaller windows are required to detect the finer-grained patterns of topography and 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 within a square quadrat, which was translated across the area of interest in steps of one pixel. Land-cover maps showing seasonal land-cover regions (Loveland *et al.*, 1995) were obtained in grid (raster) format from the U.S.G.S. through the global land cover characterization (GLCC) project (Loveland *et al.*, 2000).[1] The maps have a nominal 1-km spatial resolution and were derived from satellite (AVHRR) imagery over the time period April 1992 to March 1993. The global thematic resolution is *c.* 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 × 27 pixels) was centred 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 (1949) index 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 (P_i) of the i

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[1] We used Version 2 of the GLCC data base that is available at http://edcdaac.usgs.gov/glcc/glcc.html.

different land-cover types in a quadrat as:

$$I = 1 - \Sigma P_i^2 \quad (1)$$

The index I ranges from 0 to 1 with a larger index value indicating greater land-cover diversity. We note that Peet (1974) suggested that Simpson's index is of a type that is more sensitive to changes in the common land-cover types, and that other diversity indices are available (e.g. Magurran, 1988), and thus our estimate of land-cover diversity should be considered only a first-order measure of biodiversity.

The observed land-cover diversity is shown in Fig. 3. 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). The land-cover diversity distributions for each of the five provinces are non-Gaussian with negative skewness (large tails below the mean value). The skewness values are particularly large for the Madrean Archipelago and Sierra Madre provinces. Many factors may be contributing to skewed distributions; in desert environments, topographic and edaphic control of land-cover patterns may be especially strong, but in desert coastal and riparian systems, the existence of water could mask or even obviate other driving variables (Wiens *et al.*, 1985). In a comparative study of the biodiversity of Yellowstone and Patagonia, Barnosky *et al.* (2001) showed that local circumstances including history significantly alter patterns that might be predicted from continental-scale correlations. We attempted to control the influence of human land-use history by focusing on semi-natural vegetation types, but even natural patterns will depend on the specific history of regional species movement and local opportunistic persistence over millennia.

QUANTITATIVE TOPOGRAPHIC ANALYSIS: METHOD

Evaluation of the relationship between topography and biodiversity requires a method to extract quantitative measures of the topography. Basic statistical information such as the mean and standard deviation of the elevation distribution can be supplemented by information about the topographic fabric, namely orientation, organization and roughness. A DEM is a gridded data set of elevations that it well suited to numerical evaluation. DEMs exist over a wide range of spatial scales, from the small-scale global coverage to large-scale local coverage (see e.g. the Digital Elevation Data Catalog at http://www.geo.ed.ac.uk/home/ded.html).

In this study, a 30-arcsec DEM (providing a spatial resolution of *c.* 1 km) was used to create a terrain classification data set based on several characteristics of the topography including mean elevation, gradient, slope aspect, grain orientation, organization and roughness. The synthetic slope organization (SSO) method (Chapman, 1952; Guth *et al.*, 1987; Guth, 1995) was used to quantify the topographic fabric. Briefly, this method is based on an eigenvalue analysis of the surface normals in a moving window that covers the DEM of interest. The surface normals can be viewed as a cloud of vectors in space, and the three eigenvectors (computed from a 3×3 matrix of the sums of the cross-products of the directional cosines of the surface normals at each point in the DEM) define the three-dimensional ellipsoid that best models their distribution. The relative magnitudes of the three eigenvectors, and their orientation, define the distribution. For topography, eigenvector S_1 is approximately vertical, and orthogonal eigenvectors S_2 and S_3 are horizontal with $S_1 \gg S_2 \sim S_3$. The eigenvector S_3 points in the direction of dominant topographic fabric and provides information about the dominant topographic orientation. The eigenvector ratios $R_1 = 1/[\ln(S_1/S_2)]$ and $R_2 = \ln(S_2/S_3)$ provide information about the roughness and organization (or the strength of the grain), respectively. The ratio R_1 correlates highly with relief, standard deviation of elevation, average slope and standard deviation of slope (all of which have traditionally been used to measure topographic roughness).

QUANTITATIVE TOPOGRAPHIC ANALYSIS: DISCUSSION OF RESULTS

Figure 4 illustrates the areal variation in the topographic orientation, organization and roughness computed using the SSO algorithm discussed above within a 10 km × 10 km window. The histograms of the distributions (Fig. 5) reveal that many of the distributions have elongated tails (particularly in the case of organization and roughness). Because a great deal of information can be 'hidden' in these tails, consideration of the kurtosis value of the distribution can be useful. We begin with a discussion of the information contained in Fig. 4 and proceed in the following section to a discussion of the predicted biodiversity map constructed from this information.

Topographic fabric

The orientation of the topographic fabric in the south-west is primarily controlled by crustal deformation in response to tectonic motion between the North American and Pacific plates. Interplate stresses have resulted in boundary-parallel topographic fabric (most evident in the California Coastal Ranges and the Baja California Peninsula). This observation is corroborated by the good correlation of NW–SE regional orientation of the topographic fabric within the five provinces with their proximity to the North American–Pacific plate boundary. In general, the strength of the topographic fabric with the various provinces reflects the degree of active tectonics. In the relatively undeformed Colorado Plateau, the topographic coherency is poor (standard deviation of 28° about the mean N–S fabric orientation) and the topography is relatively poorly organized (0.79). In contrast, topography along the Rio Grande Rift (the most tectonically active province) is closely distributed about the mean N–S orientation (with a standard deviation of *c.* 12°) and has a relatively high degree of organization (1.07). The orientation of the topographic grain in provinces geographically closer to the

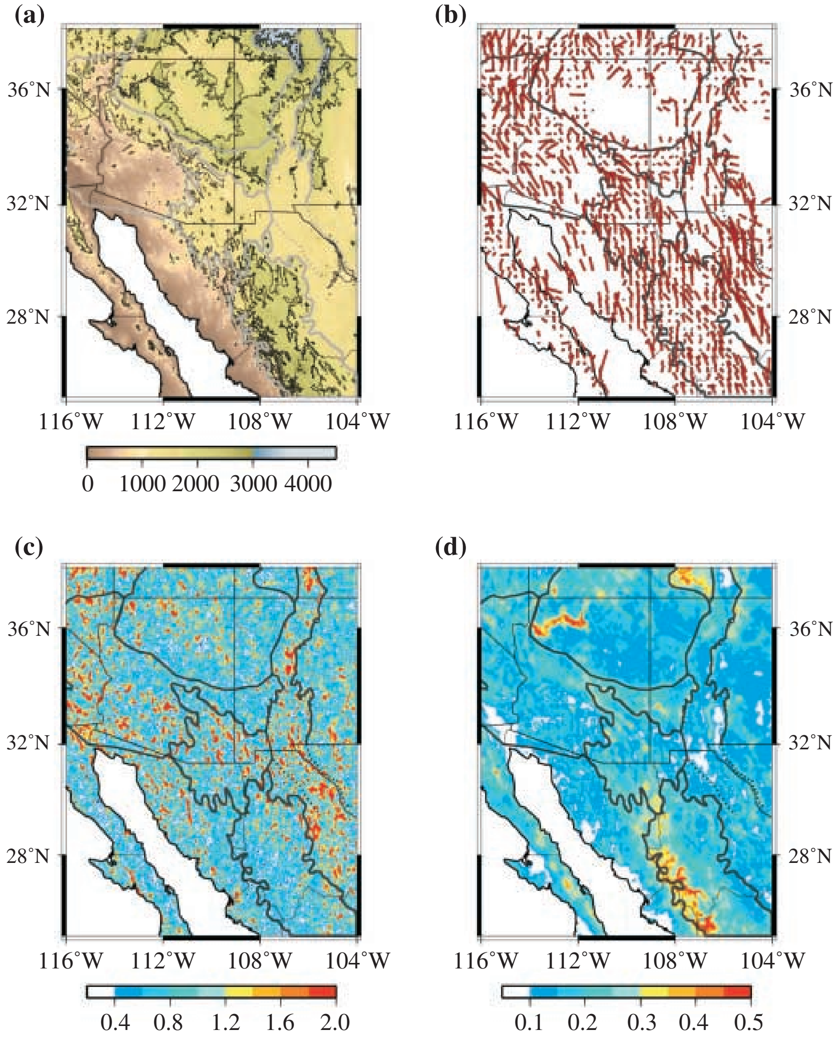

Figure 4 Spatial distribution of various descriptive topographic quantities for the south-western US calculated using the algorithms discussed in the text. (a) Topography of the study area overlain with the 1000 m contour interval. (b) Vectors of the topographic fabric orientation computed for the topography with a moving 20 km × 20 km window. Vector lengths are scaled by organization with longer vectors indicating greater organization. A flatness cut-off was used to omit topographic grain vectors for areas of little topographic relief. The resulting vector plot is therefore the topographic grain of elevated regions. (c) Topographic organization computed within a moving 10 km × 10 km window. (d) Topographic roughness computed within a moving 10 km × 10 km window.

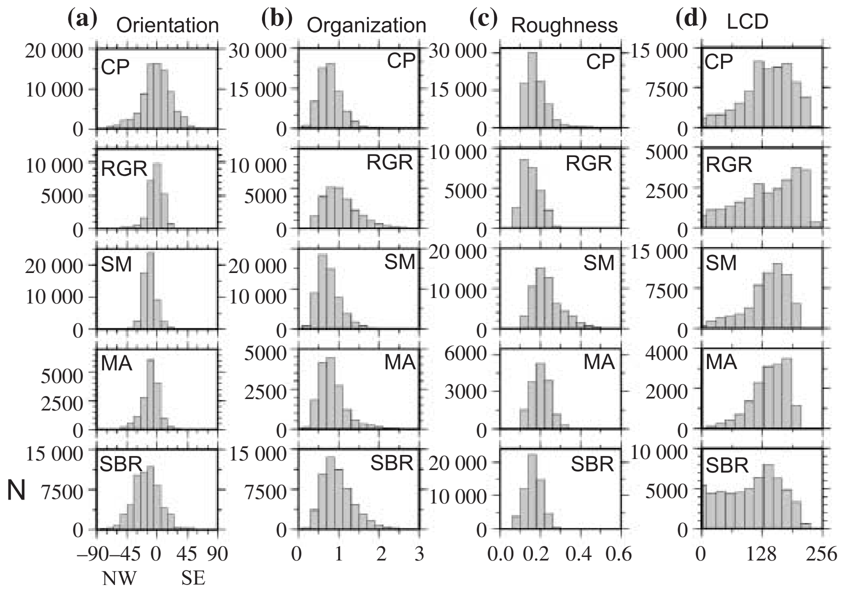

Figure 5 Histograms of the orientation, organization, roughness and land-cover diversity for the five tectonic provinces of the south-western US Cordillera as shown in Fig. 1. Values for the mean, standard deviation, skewness and kurtosis are listed in Table 1.

plate margin (Sierra Madre, Madrean Archipelago, and Southern Basin and Range) are rotated the NW, subparallel to the relative motion between the North American and Pacific plates. We find a high coherence of the topographic grain within the Sierra Madre and Madrean Archipelago provinces that are also characterized by low standard deviations about the mean grain orientation. We attribute the low level of topographic organization in the Sierra Madre province to the high level of drainage-related incisement present in this region; in general, the development of drainage networks has the effect of lowering the organization relative to topography of tectonically active areas. Finally, we note that the distributions are all skewed towards higher organization, indicating the existence of highly organized topographic regions within each of the provinces. The kurtosis of the topographic organization within each of the five provinces is leptokurtic (positive), indicating small tails about the mean values.

Topographic roughness

Topographic roughness correlates well with other measurements (e.g. relief, standard deviation of elevation, average slope and standard deviation of slope), and a number of tectonic and geomorphic processes contribute to roughness values including high heat flow, erosion and incision rates. Because no single process is responsible for roughness, it is difficult to correlate the distributions in Fig. 4. Nevertheless some generalizations are possible. The same drainage-related incisement processes responsible for lowering the organization of the Sierra Madre province result in a high degree of roughness relative to the other provinces (0.26 vs. *c.* 0.18 and 0.20). The Colorado Plateau has a low mean roughness value (0.18), which is also evident in Fig. 4 (with the obvious exception of the very rough Grand Canyon region – which has the largest roughness value in the data set). The distribution for this province is characterized by a large kurtosis value (5.5), indicative of a sharp mean peak. Similarly, the Rio Grande Rift, dominated by the relatively smooth rift valley, shows a relatively low roughness values (0.16), although the negative kurtosis value for the distribution indicates significant spread about the mean value reflecting the existence of rough escarpments along the margin of the rift. We note that all the provinces have similar standard deviations values, indicating similar distribution widths about the mean roughness values. The distributions for the Colorado Plateau and the Sierra Madre provinces are skewed towards higher roughness, suggesting the existence of rough outliers in the distribution.

Land-cover diversity

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 towards 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 centres 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.

PREDICTED BIODIVERSITY

The construction of a predicted biodiversity map based on the topographic information is based on our hypothesis that in many parts of the south-west high levels of biodiversity correlate with topography exhibiting the following characteristics: (1) high roughness, which encourages the vertical stack 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 *c.* 1500 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 (Fig. 1). We have adopted the simplest approach, using an unweighted sum of normalized values of these topographic quantities to construct a predicted biodiversity map for the study area. The resulting data base (Fig. 6a) is renormalized and compared with the normalized observed land-cover diversity data base (Fig. 6b). The spatial variations in the misfit between the predicted and observed biodiversity data sets is shown in Fig. 6c, 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 (Fig. 6d).

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 (Fig. 6c) shows good agreement between the predicted and observed biodiversity throughout much of the Sierra Madre and Madrean Archipelago provinces. The biodiversity is overestimated in much of the central Colorado

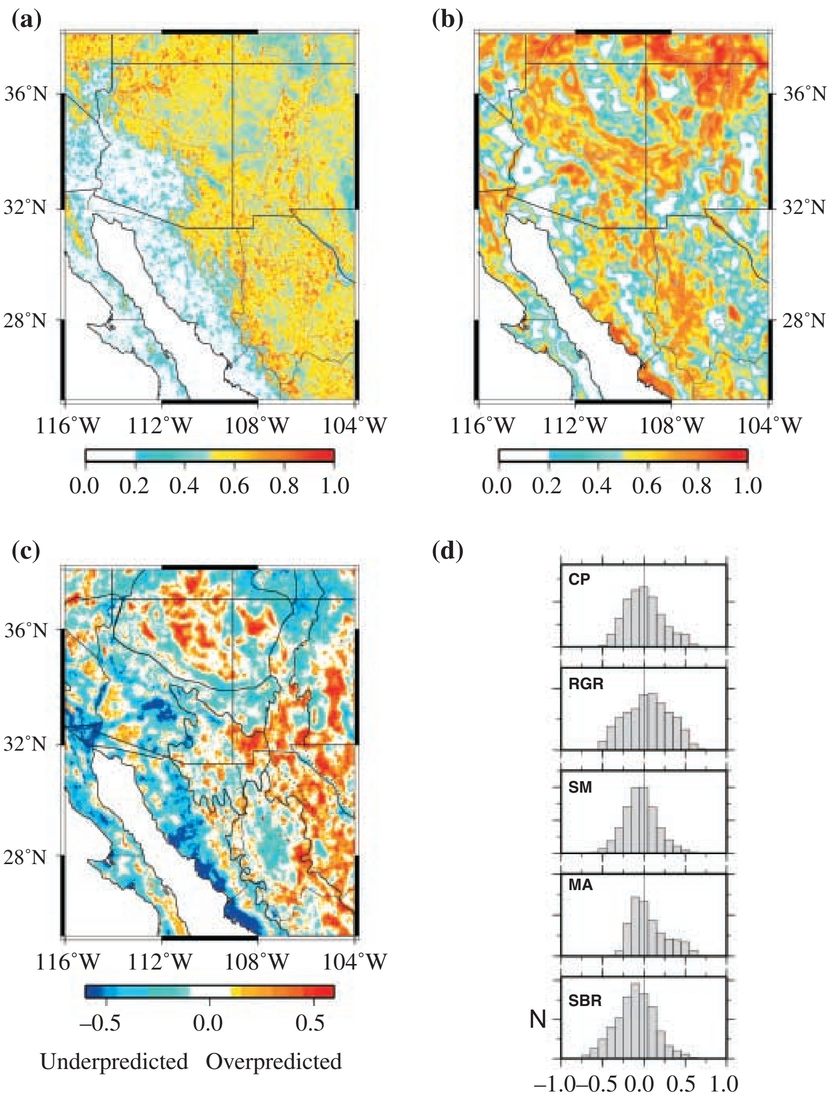

Figure 6 (a) Predicted biodiversity based on the topographic analysis algorithm discussed in the text. (b) Normalized observed biodiversity based on the land-cover diversity data set. (c) Misfit values of the difference between the predicted and observed data sets. Red and blue regions designate regions where the biodiversity has been over- and under-predicted, respectively. (d) Histograms of the misfit for the five topographic provinces.

Plateau, the eastern section of the Madrean Archipelago, the southern Rio Grande Rift, and the region to the east of the Sierra Madre. 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.

Within the individual provinces the misfit distributions are remarkably Gaussian with mean values very close to zero. The Rio Grande Rift and Southern Basin and Range provinces have very low skewness (< 0.05) in contrast to the other provinces that are significantly skewed to positive (overestimation) misfit values. With the exception of the Rio Grande Rift province (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 < 0.1). We note, however, that only a weak linear correlation exists between the calculated and observed values for the province-wide distributions (R^2 values < 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 nonlinear 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 large regions of poor correlation between prediction and observation that prevents the establishment of high R^2 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 (Austin *et al.*, 1984; Austin, 1985; Austin & Smith, 1989). 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 south-west, 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 & Niering, 1965, 1968; Brown & 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 & Wilson, 1994), this is quantifiable in terms of the topographic roughness which 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 geographical 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 data bases are available. We note that in the south-west the role of soil diversity can be expected to have a profound effect on the biodiversity given the complex geologic history which has resulted in the superimposition of sequences of pre-Cambrian igneous, Palaeozoic 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 time-scales long enough to take climatic change into account. In particular, over the past 2 Myr 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 (Noble, 1993; Allen & 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 short-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. Gardner *et al.*, 1987; Wiens & Milne, 1989; Milne, 1991; Levin, 1992; Allen *et al.*, 1999; Siemann & Brown, 1999; Allen & Holling, 2002; Peterson, 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

Topography is a fundamental geophysical observable that contains valuable information about the geodynamic, tectonic and climatic history of a region. It is also by far the most readily measurable and accurately known of all the parameters used to describe the Earth. As a consequence, topographic features have historically invited many studies that have sought to extract the information contained in the ‘character’ of the Earth’s surface. Recent advances in computing capabilities, availability of high-resolution DEMs, and the recent assembly of a land-cover diversity map which to a first-order can be used to approximate the distribution of biodiversity have motivated this evaluation of the relationship between topography and the spatial distribution of biodiversity. In this paper, we have tested the hypothesis that a combination of three measurable topographic quantities (organization, roughness and mean elevation) exerts an important control on the spatial biodiversity distribution.

Within the underlying assumptions of this study 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 data sets.

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.

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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. & Holling, C.S. (2002) Cross-scale structure and scale breaks in ecosystems and other complex systems. *Ecosystems*, **5,** 315–318.

Allen, R.B. & Peet, R.K. (1990) Gradient analysis of forest of the Sangre de Cristo Range, Colorado. *Canadian Journal of Botany*, **68,** 193–201.

Allen, R.B., Peet, R.K. & Baker, W.L. (1991) Gradient analysis of latitudinal variation in Southern Rocky Mountain forests. *Journal of Biogeography* **18,** 123–139.

Allen, C.R., Forys, E.A. & Holling, C.S. (1999) Body mass patterns predict invasions and extinctions in transforming landscapes. *Ecosystems*, **2,** 114–121.

Austin, M.P. (1985) Continuum concept, ordination methods and niche theory. *Annual Review of Ecology and Systematics*, **16,** 39–61.

Austin, M.P. & Smith, T.M. (1989) A new model for the continuum concept. *Vegetatio*, **83,** 35–47.

Austin, M.P., Cunningham, R.B. & Fleming, P.M. (1984) New approaches to direct gradient analysis using environmental scalars and statistical curve fitting procedures. *Vegetatio*, **55,** 11–27.

Barnosky, A.D., Hadly, E.A., Maurer, B.A. & Christie, M.I. (2001) Temperate terrestrial vertebrate faunas in North and South America: interplay of ecology, evolution, and geography with biodiversity. *Conservation Biology*, **15,** 658–674.

Behle, W.H. (1978) Avian biogeography of the Great Basin and Intermontane Region. *Great Basin Naturalist Memoirs*, **2,** 55–80.

Brown, J.H. (1971) Mammals on mountaintops: nonequilibrium insular biogeography. *American Naturalist*, **105,** 467–478.

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

Brown, D.E. (ed.) (1982) Biotic communities of the American southwest United States and Mexico. *Desert Plants*, **4,** 1–342.

Brown, J.H. & Gibson, A.C. (1983) *Biogeography*. p. 641. Mosby Co., London.

Brown, D.E. & Lowe, C.H. (1980) *Biotic communities of the southwest*. USDA Forest Service General Technical Report, RM-78.

Burke, I.C. (1999) Spatial variability of soil properties in the shortgrass steppe: the relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems*, **2,** 422–438.

Chapman, C.A. (1952) A new quantitative method of topographic analysis. *American Journal of Science*, **250,** 428–452.

Cole, K.L. (1982) Late Quaternary zonation of vegetation in the eastern Grand Canyon. *Science*, **217,** 1142–1145.

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. *Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico* (ed. by F. Leonard DeBano, P.F. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre and C.B. Edminster, technical coordinators), 19–23 September, pp. 36–59. General Technical Report RM-GTR-264, Tucson, AZ. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

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.

Gosz, J.R. & Sharpe, P.J.H. (1989) Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. *Landscape Ecology*, **3,** 229–243.

Guth, P.L. (1995) Slope and aspect calculations on gridded digital elevation models: examples from a geomorphometric toolbox for personal computers. *Zeitschrift fur Geomorphologie N.F. Supplementband*, **101,** 31–52.

Guth, P.L., Ressler, E.K. & Bacastow, T.S. (1987) Microcomputer program for manipulating large digital terrain models. *Computers and Geosciences*, **13,** 209–213.

Hanawalt, R.B. & Whittaker, R.H. (1976) Altitudinally coordinated patterns of soils and vegetation in the San Jacinto Mountains, California. *Soil Science*, **121,** 114–124.

Hansen, A.J. & Rotella, J.R. (1999) Abiotic factors and biodiversity. *Maintaining biodiversity in forest ecosystems* (ed. by M. Hunter), p. 714. Cambridge University Press, Cambridge.

Hastings, J.R., Turner, R.M. & Warren, D.K. (1972) *An atlas of some plant distributions in the Sonoran Desert*. University of Arizona Press, Tucson.

Heald, W. (1967) *Sky island*, p. 166. University of Arizona Press, Tucson.

Huggett, R.J. (1995) *Geoecology: an evolutionary approach*, p. 320. Routledge, London.

Johnson, N.K. (1978) Patterns of avian biogeography and speciation in the intermountain regions. *Great Basin Naturalist Memoirs*, **2,** 137–160.

Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73,** 1942–1968.

Loveland, T.R., Merchant, J.W., Brown, J.F., Ohlen, D.O., Reed, B.C., Olson, P. & Hutchinson, J. (1995) Seasonal land-cover regions of the United States. *Annals of the Association of American Geographers*, **85,** 339–355.

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.

McCoy, E.D. & Connor, E.F. (1980) Latitudinal gradients in the species diversity of North American mammals. *Evolution*, **34,** 193–203.

McLaughlin, S. (1994) An overview of the flora of the sky islands, southeastern Arizona: diversity, affinities, and insularity. *Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico* (ed. by F. Leonard DeBano, P.F. Ffolliott, A. Ortega-Rubio, G.J. Gottfried, R.H. Hamre and C.B. Edminster, technical coordinators), 19–23 September 1994, pp. 60–70. General Technical Report RM-GTR-264, Tucson, AZ. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Magurran, A.E. (1988) *Ecological diversity and its measurement*, p. 192. Princeton University Press, Princeton.

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.

Merriam, C.H. (1894) Laws of temperature control of the geographic distribution of terrestrial animals and plants. *National Geographic*, **6,** 229–238.

Milne, B.T. (1991) Lessons from applying fractal models to landscape patterns. *Quantitative methods in landscape ecology* (ed. by M.G. Turner and R.H. Gardner), pp. 199–235. Springer-Verlag, New York.

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.

Patterson, B.D. (1980) Montane mammalian biogeography in New Mexico. *Southwestern Naturalist*, **25,** 33–40.

Peet, R.K. (1974) The measurement of species diversity. *Annual Reviews of Ecology and Systematics*, **5,** 285–307.

Peet, R.K. (1978) Latitudinal variation in Southern Rocky Mountain forests. *Journal of Biogeography*, **5,** 275–289.

Peterson, G.D. (2002) Contagious disturbance, ecological memory, and the emergence of landscape pattern. *Ecosystems*, **5,** 329–338.

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.

Simpson, B.B. (1975) Pleistocene changes in the flora of the high tropical Andes. *Paleobiology*, **1,** 273–294.

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. *Packrat Middens: The last 40,000 years of biotic change* (ed. by J.L. Betancourt, T.R. Van Devender and P.S. Martin), pp. 134–164. The University of Arizona Press, Tucson.

Vuilleumier, F. (1970) Insular biogeography in continental species. I. The North Andes of South America. *American Naturalist*, **104,** 373–388.

Warshall, P. (1994) The Madrean sky island archipelago: a planetary overview. *Biodiversity and management of the Madrean Archipelago: the sky islands of southwestern United States and northwestern Mexico* (ed. by F. Leonard DeBano, Peter F. Ffolliott, Alfredo Ortega-Rubio, Gerald J. Gottfried, Robert H. Hamre and Carleton B. Edminster, technical coordinators), 19–23 September, pp. 408–415. General Technical Report RM-GTR-264, Tucson, AZ. US Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

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. *Evolutionary biology 10* (ed. by M.K. Hect, W.C. Steere and B. Wallace), pp. 1–67. Plenum Press, New York.

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.

Whittaker, R.H. & Niering, W.A. (1968) Vegetation of the Santa Catalina Mountains, Arizona. IV. Limestone and acid soils. *Journal of Ecology*, **56,** 523–544.

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.

Wiens, J.A., Crawford, C.S. & Gosz, J.R. (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos*, **45,** 421–427.

BIOSKETCHES

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