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Diversity of ecological communities of the United States

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Abstract

Biodiversity, although recognized as encompassing several levels of biological organization, is often thought of as species diversity. Three diversity estimates were calculated for the conterminous United States using satellite data acquired from the Advanced Very High Resolution Radiometer (AVHRR): land cover richness, vegetation richness, and vegetation clustering. Vegetation richness and vegetation clustering showed a scale-dependent relationship to elevation across the range of quadrat sizes from 500 to 50,000 mi^2. All diversity measures increased east to west, with a rather abrupt transition at the Colorado Front Range. The longitudinal diversity gradients found in this study are in contrast to the reported latitudinal and longitudinal gradients for species diversity.

Introduction

A commonly accepted definition of biodiversity (Noss 1990; Cooperrider 1990; Stoms & Estes 1993) is "the variety and variability of life and the ecological complexes in which they occur" (U.S. Congress, Office of Technology Assessment (OTA) 1987). Public concern and scientific interest has emphasized species in biodiversity research and preservation, perhaps because of the emphasis placed on species in the U.S. Endangered Species Act of 1973 (Public Law 93–205). Relatively little effort has been focused on the diversity of ecological communities. Although others have noted that biodiversity has an ecosystem component (OTA 1987; Noss 1990, West 1993), the number and distribution of ecological communities in an area is typically not thought of as a measure of biodiversity. The lack of research on diversity at levels of organization above species has been noted by others (Noss & Harris 1986, Belbin 1993).

The purpose of this paper is to examine patterns of diversity of ecological communities across the subcontinental region of the conterminous United States. Diversity of ecological communities is important because of the economic goods and services which it provides (Westman 1977; Walker 1992; West 1993; USEPA 1994). Some examples include low-cost clean water, stable beaches, and recreation, in addition to species habitat. Many of these economic benefits are not supplied by the species themselves, but rather by the diversity of the terrestrial and aquatic environments in which they live.

Ecological communities are represented using the United States Geological Survey's (USGS) land cover characteristics data base (Loveland *et al.* 1991). Mapping is based on the combination of Advanced Very High Resolution Radiometer (AVHRR) satellite data at 1 km^2 spatial resolution and geographic data in a Geographic Information System (GIS). The principal ancillary (GIS) data are elevation, climate, ecoregions, land cover, and land resource areas (Brown *et al.* 1993).

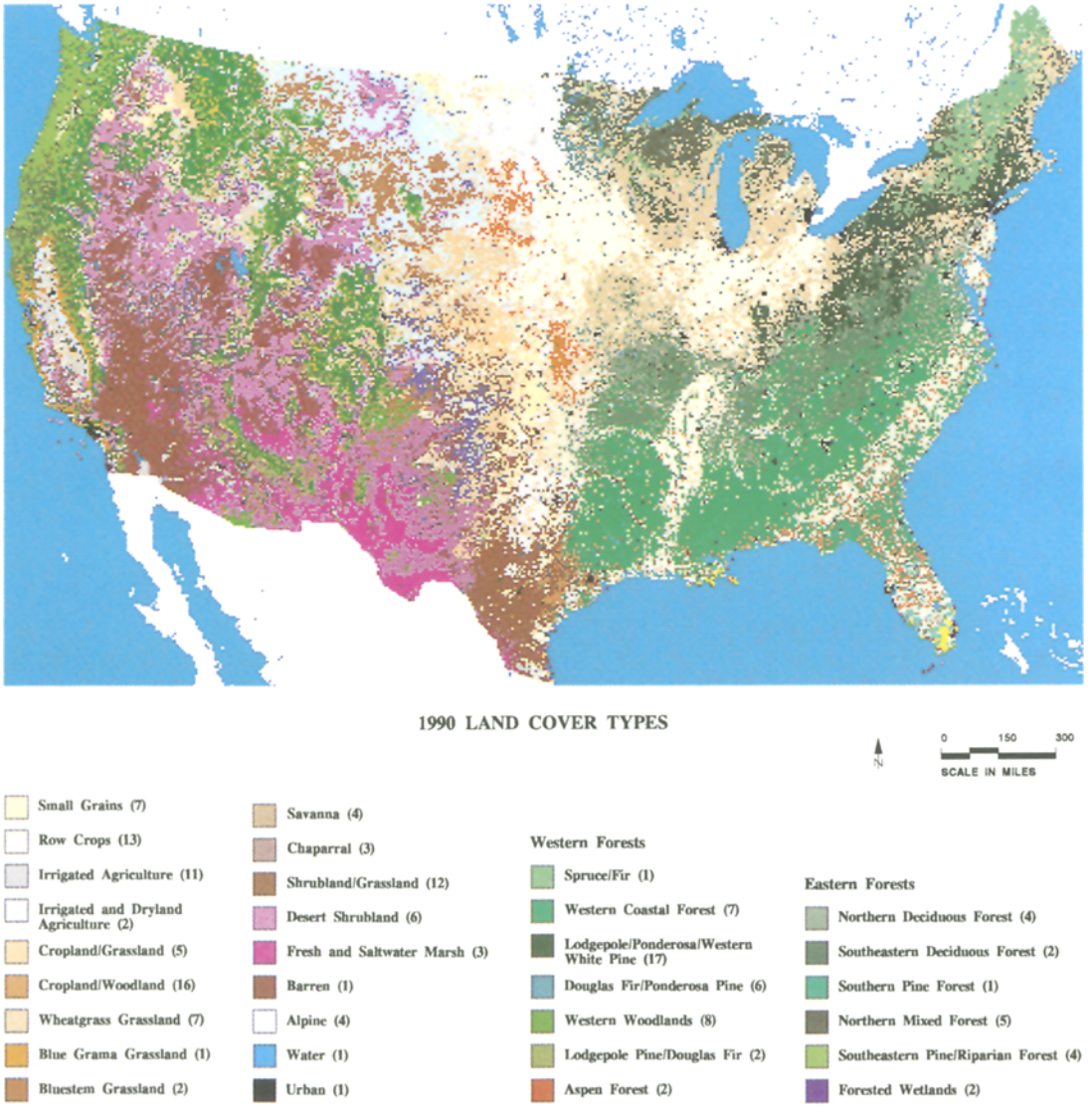

Fig. 1. Land cover and vegetation map of the conterminous United States (adapted from Loveland *et al.* 1991)

Methods

The land cover characteristics data (Loveland *et al.* 1991) contain 159 classes. The classes are different combinations of agriculture and natural vegetation. Loveland (personal communication) added urban data, providing a 160-class land cover characteristics data set. A simplified version (by the authors) is shown in Figure 1, with the accompanying legend in Table 1. The simplification was done by aggregating the 160 categories into logical groups. For example, the western woodlands category listed in Table 1 is an aggregation of eight different classes that were various combinations of ponderosa, pinyon, and western white pines, juniper, sage species, and grasses. The simplification was done only for presentation of Figure 1, since the eye cannot perceive 160 different colors. The 160-class data set was used in this study.

The land cover characteristics data were resampled to 10 km pixels, and converted to points. Resampling from 1 km to 10 km pixels was done to reduce the number of points in each quadrat to a manageable number; it does not change the proportion of classes from that of the original map (Lillesand & Kiefer 1987). Points lying outside the continental boundaries of a 1:2,000,000-scale data set of the United States (ESRI

1992) were eliminated. The point data were then overlaid in a GIS onto a series of regular grids made up of quadrats of varying size. The grids were created in a Lambert Azimuthal Equal Area projection using ARC/INFO GIS software. The Lambert Azimuthal Equal Area projection was chosen because it was the projection used for the Loveland *et al.* (1991) land cover characteristics data. Also, by using an equal area projection, each quadrat contained approximately the same number of points, excluding quadrats along continental margins (e.g. political boundaries, coastlines). Equal area is a property of all azimuthal projections (Snyder 1987). The center of projection is 45°00′00″N and 100°00′00″W.

This type of square grid structure has been commonly used for continental scale studies of species richness (Simpson 1964, Kiester 1971, Schall & Pianka 1978; Currie 1991). The continental scale studies of species richness cited above used fixed-size quadrats. One of the central tenets of landscape ecology is that ecological relationships are scale-dependent (Risser *et al.* 1984, Naveh & Lieberman 1984, Forman & Godron 1986). The series of grids with varying quadrat size was created because we hypothesized that correlations between diversity estimates and independent variables would change based on the size of the quadrats on which diversity and independent variables were calculated.

Quadrat size ranged from 500 mi^2 up to 50,000 mi^2 in increments of 500 mi^2 between 500 and 11,000 mi^2, and increments of 1,000 mi^2 thereafter (Table 1). Five hundred mi^2 increments were used below the quadrat size of 11,000 mi^2 to better define the trend between diversity measures and independent variables. The number of observations decreased from 5,874 at a quadrat size of 500 mi^2 to 58 at a quadrat size of 50,000 mi^2.

Three measures of diversity were created by overlaying land cover points in the quadrats. For each quadrat the number of different land cover types was summed. The number of different land cover types by quadrat is a measure of land cover type richness.

A second summation was created by weighting the land cover types by whether or not it had an agricultural or urban label. Classes that were entirely agriculture or urban were given a weight of zero (0). Classes that were a mixture of natural and agricultural vegetation (e.g. the cropland/woodland category in Table 1) were given a weight of one, and classes that were natural vegetation were given a weight of two. The number of different weighted land cover types was computed for each quadrat. This weighting scheme gives a measure of vegetation type richness for each quadrat, as opposed to land cover type richness, since points that are agriculture or urban are multiplied by zero.

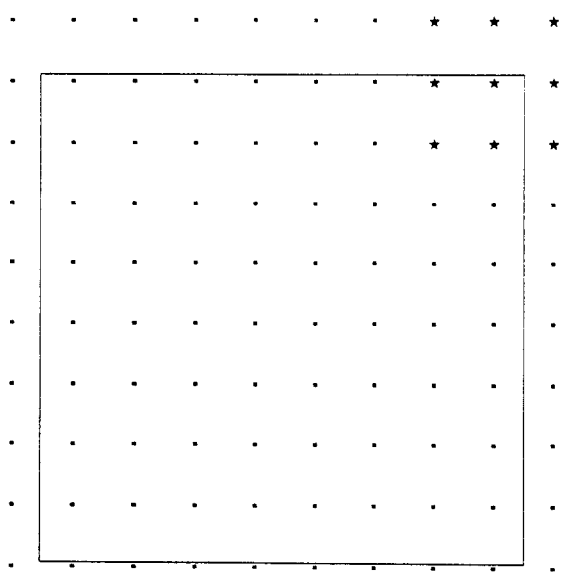

Fig. 2. Calculation of vegetation cluster scores. Points shown as stars highlight search method to calculate cluster score for each point.

A third measure of diversity was created by looking at the variety of vegetation types surrounding each point. The eight nearest neighbors were searched around each point and summed according to the above weights to provide a score for that point. The maximum score for a given point was 18, which occurred when all eight nearest neighbors, plus the center point itself, were different natural cover types. The total for a quadrat was then calculated by summing the scores for each point within that quadrat. Quadrat boundaries were ignored in calculating the score for each point (Figure 2). Higher scores indicate a greater number of different vegetation types within a 9×9 neighborhood, providing a measure of vegetation clustering.

Elevation range, topographic clustering (USGS 1990), and stream density (ESRI 1992) from 1:2,000,000-scale map data were also computed for each quadrat. These data were included as independent variables in regression models to determine if any relationship existed between these variables and the vegetation richness and vegetation clustering diversity measures. Elevation range and topographic clustering were chosen because previous studies have shown veg-

Table 1. Quadrat Sizes.

Cell Size	Side Length	Cell Size	Side Length	Cell Size	Side Length
500	22.4	10000	100.0	30000	173.2
1000	31.6	10500	102.5	31000	176.1
1500	38.7	11000	104.9	32000	179.9
2000	44.7	12000	109.5	33000	181.7
2500	50.0	13000	114.0	34000	184.4
3000	54.8	14000	118.3	35000	187.1
3500	59.2	15000	122.5	36000	189.7
4000	63.3	16000	126.5	37000	192.4
4500	67.1	17000	130.4	38000	194.9
5000	70.7	18000	134.2	39000	197.5
5500	74.2	19000	137.8	40000	200.0
6000	77.5	20000	141.4	41000	202.5
6500	80.6	21000	144.9	42000	204.9
7000	83.7	22000	148.3	43000	207.4
7500	86.6	23000	151.7	44000	209.8
8000	89.4	24000	154.9	45000	212.1
8500	92.2	25000	158.1	46000	214.5
9000	94.9	26000	161.3	47000	216.8
9500	97.5	27000	164.3	48000	219.1
		28000	167.3	49000	221.4
		29000	170.3	50000	223.6

etation change along elevational gradients in both the eastern and western United States (Whittaker 1956, 1960; Whittaker & Niering 1965). Others have noted that streams initiate a mesic to xeric gradient across the landscape (Odum 1978; Kauffman & Krueger 1984; Gregory *et al.* 1991), which, in turn, should initiate vegetation change from riparian to upland formations.

Elevation range was calculated as the difference between the highest and lowest elevation in the quadrat. Stream density was calculated as the total stream length per quadrat. Topographic clustering was created using the same logic and methods that were used to calculate vegetation clustering. Each elevation point was rounded to the nearest 100 feet so that each point had an elevation that was a multiple of 100. The eight nearest neighbors were then searched around each point and summed according to the number of different elevation values. If all eight nearest neighbors and the center point itself had a different elevation, that point would receive a maximum score of nine. The total for the quadrat was calculated by summing the score for each point. Quadrat boundaries were again ignored in computing topographic clustering for each point (see Figure 2).

Regression analyses were performed at each quadrat size to determine if aspects of topography and the abundance of streams explained regional variation in vegetation richness and vegetation clustering, and to determine if the relationships changed as a function of quadrat size. To minimize the impact of continental margins only quadrats with 50 percent or more of the possible points for that quadrat size were included. Vegetation richness and clustering scores for these quadrats were then normalized by dividing by the number of points in the quadrat. Regression analyses were conducted using the normalized scores.

The independent variables were log-transformed because of non-normal distributions. Topographic clustering and stream density were not used in the regression models. Topographic clustering was strongly correlated with elevation range at all quadrat sizes ($r \geq 0.90$); and stream density showed only weak correlations with the diversity measures at all quadrat sizes. The polynomial in equation 1 provided the best fits

over the range of quadrat sizes examined:

$$V = a - b(E) + c(E^2) + e \qquad (1)$$

where V is vegetation richness or clustering, E is log-transformed elevation range, a, b, and c are parameter estimates, and e is the error term.

Isoline maps were created for each of the diversity measures by inspecting the trend in R-square values versus quadrat size. The orignal diversity measures, not the normalized scores, were used to make the isoline maps. The isoline maps were created by screen digitizing each isoline with the quadrat scores displayed in the background. Manual construction also allowed us to ignore quadrats that had artificially low scores because they were along a coast or other boundary.

Results

The results of the regression analyses are shown in Figure 3. The change in R-square values with quadrat size for vegetation richness exhibits an asymptotic behavior similar to a species-area curve. R-square values increase dramatically from 500 to 5,000 mi^2 quadrats, then increase more slowly from 5,000 to about 11,000 mi^2. An asymptote is reached between 11,000 to 13,000 mi^2. The most dramatic increase in R-square values was between 500 and 1,000 mi^2.

There is also change from a more steep to a more gentle slope at approximately 5000 mi^2 for vegetation clustering, but an asymptote is not apparent across the range of quadrat sizes examined. The lack of a clear asymptote is partly the result that vegetation clustering scores increased with each increase quadrat size. Presumably, there is an upper limit to vegetation clustering scores such that an asymptote would be reached at larger quadrat sizes. However, each increase in quadrat size reduces the number of observations in the regression model. At quadrat sizes larger than 50,000 mi^2, the number of observations would have become limiting.

The "bumpiness" in R-square values versus quadrat size for vegetation richness and vegetation clustering above approximately 10,000 mi^2 is the result of the change in the size and positioning of the quadrats. There were about five quadrats with relatively high diversity scores and low elevation ranges. Depending on how the quadrats captured these areas, their effect as outliers was sometimes more extreme, which reduced R-square values.

Isoline maps for land cover richness, vegetation richness, and vegetation clustering were made using the 13,000 mi^2 quadrat. This quadrat size was chosen because it had the highest R-square value in the asymptote region (see above) for vegetation richness. Each isoline map shows a general pattern of increasing diversity from east to west.

The land cover richness map (Figure 4) shows scores increasing from 15 in the east to above 45 in the west. There is one island with a land cover richness score above 30 in the Mississippi River Valley, and four above 45 in the west. There are also several depressions, including southern California along the border with Nevada, southwestern Texas, Iowa and southern Minnesota, the Appalachians, and the Gulf Coast.

The vegetation richness isoline map (Figure 5) shows a similar pattern to the land cover richness map (Figure 4). Scores are 20 or less in the east and increase westward. The 40 isoline generally follows the Colorado Front Range. There are three islands of high vegetation richness in the west. These include northwestern Colorado, southcentral Washington, and northcentral California. There is also an island of high vegetation richness in southern Florida. Figure 5 also shows a large depression in the Upper Great Plains and Midwest extending south along the Appalachians. This pattern is partly due to the isoline values being inclusive. If a value of 19.5, instead of > 20, had been used to draw the isoline, this depression would have been broken into northern and southern pockets. Vegetation richness scores were 20 and above in the Appalachians.

The vegetation clustering isoline map (Figure 6) also shows scores increasing from east to west, generally increasing above 2000 west of the Colorado Front Range. Islands of high vegetation clustering in the east (above 2000) are found along the Appalachians, south Florida, the southeast from Kentucky through the Gulf States, northern Minnesota and western Arkansas. The highest vegetation clustering score (> 4000) is found in southwest Colorado.

Discussion

Differences in the diversity values found in the east versus west may be a function of the scale of the imagery used in this study and/or a function of different scaling relationships among ecological processes in the east versus the west. The diverse and varied topography in

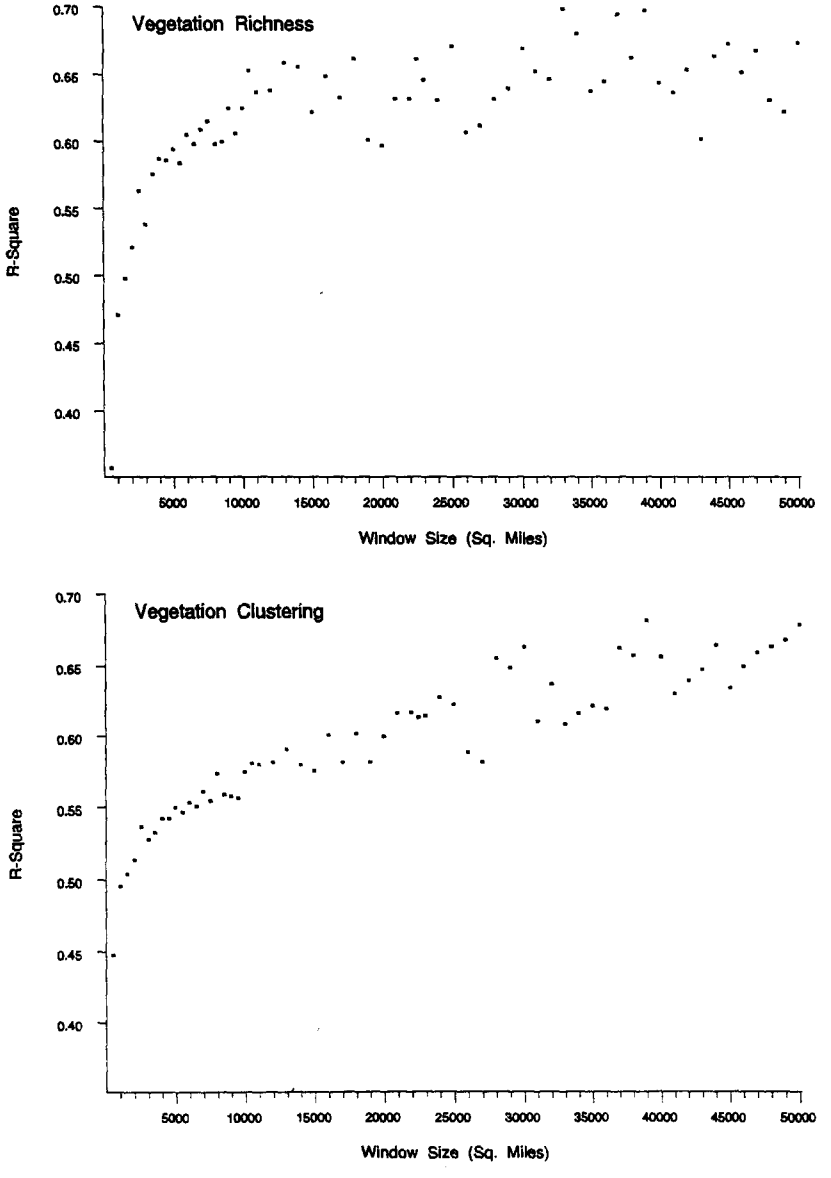

Fig. 3. R^2 Values versus quadrat size.

the west causes wide variation in temperature and precipitation extremes, as well as soil formation, which results in highly variable vegetation types within many regions of the west, but especially within mountainous areas. The eastern United States has a more gradual latitudinal gradient in climate, precipitation, and soils. This results in less abrupt transition in vegtation types at the scale of this study (as compared to the western U.S.), and, hence, fewer cover types per quadrat.

The general pattern of increasing diversity from east to west is in contrast with latitudinal gradients in species diversity at continental to global scales (Simpson 1964; Pianka 1966; Kiester 1971; Brown & Gibson 1983; Wright 1983; Currie 1991; Rohde 1992). The north-south terrestrial species gradient appears to result from a similar gradient of available energy (Brown & Gibson 1983; Wright 1983; Currie 1991; Rohde 1992). Also, the east to west gradient in vegetation diversity

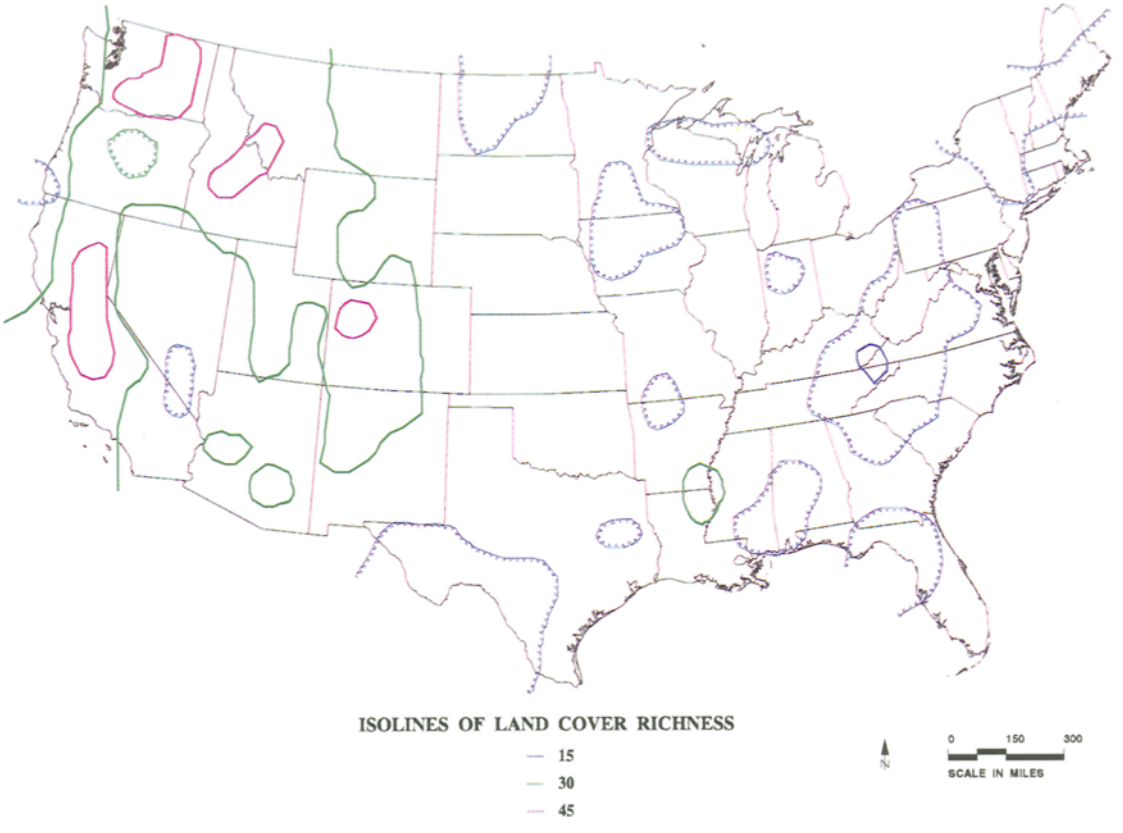

Fig. 4. Isoline map of land cover type richness. Contour values are inclusive.

found in this study is in contrast to the west to east increase in tree species diversity for North America (Currie & Paquin 1987; Currie 1991), and an increase in insectivorous bird richness east and west from mid-continent (Schall & Pianka 1978). The strong longitudinal influence (in addition to the latitudinal gradient) in tree species diversity follows a similar gradient in available moisture (Currie & Paquin 1987, see also Currie 1991). The contrast in gradient direction between this study and that by Currie & Paquin (1987) suggests that fewer species are organized into a greater number of communities in the western United States. It may also be that the high tree species diversity in the eastern United States combined with the lack of strong orographic and edaphic gradients has produced a finer scale pattern of vegetation diversity.

That streams do not contribute to variation in vegetation richness and clustering at the scale of this study is not surprising. Detailed treatment of riparian vegetation types is generally beyond the resolution of the AVHRR sensor. In the west, it is likely that some of the region-to-region variation in vegetation richness and clustering would be explained by streams. For example, mixed broadleaf riparian communities are associated with perennial and semi-perennial streams in the west, which, if included as a class, would increase vegetation richness and clustering in the grid cells in which these occurred. In the east, the Loveland *et al.* (1991) classes in the southeastern pine and riparian forest legend category (Table 1) are combinations of bottomland hardwood and cypress/gum riparian types mixed with longleaf/slash or loblolly/shortleaf pine forest types. These forest types were apparently combined in the Loveland *et al.* (1991) classification because the narrow, linear nature of the riparian types is beyond the resolution capability of the AVHRR sensor.

Summary and conclusion

Patterns of biodiversity for the conterminous United States were examined using land cover and vegetation

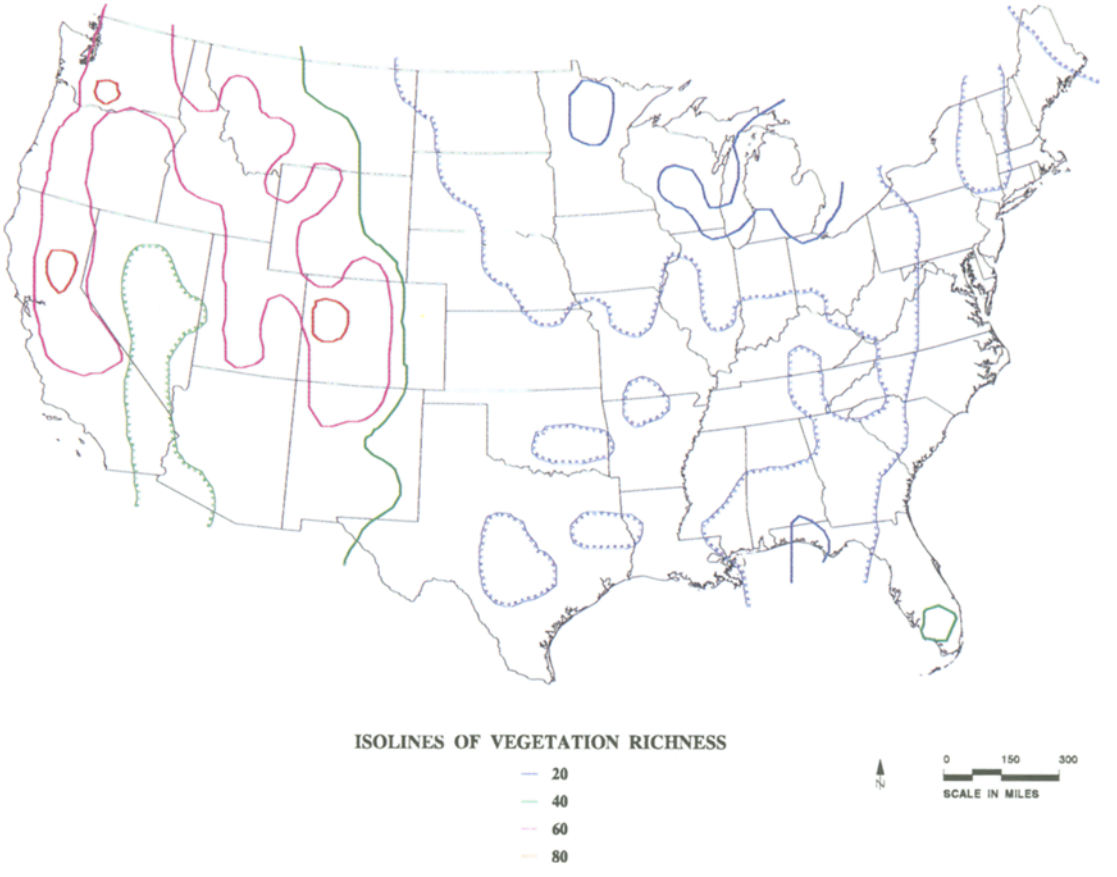

Fig. 5. Isoline map of vegetation type richness. Contour values are inclusive.

data that were generated using remote sensing and GIS technology. The diversity of vegetation, both in terms of richness and the number of different types adjacent to each other was shown to have a scale-dependent relationship with range in elevation for the continental United States. Based on these data, the correlation between vegetation richness and elevation range reached an asymptote at a scale range between 11,000 and 13,000 mi^2 (length scale of 105 to 114 miles; see Table 2). The trend in correlation between vegetation clustering and elevation range appeared to change at a quadrat size of 5,000 mi^2 (length scale of 70 miles).

Isoline maps of land cover richness, vegetation richness, and vegetation clustering showed a pattern of increasing diversity from east to west. This pattern of increasing diversity from east to west is in contrast to the numerous studies which show latitudinal and longitudinal gradients in species diversity at continental to global scales (Simpson 1964; Pianka 1966; Kiester 1971; Schall & Pianka 1978; Brown & Gibson 1983; Wright 1983; Currie & Paquin 1987; Currie 1991; Rohde 1992).

Use of remote sensing and GIS technology for biodiversity studies has been ignored (Stoms & Estes 1993). This is partly due to the focus on species in biodiversity studies. Remote sensing and GIS provide appropriate data and effective tools for studying biodiversity at levels of organization above species. Without remote sensing and GIS technology it would be more difficult to examine scaling relationships between diversity of vegetation types and environmental variables and display vegetation diversity in a format more commonly reserved for temperature and precipitation data.

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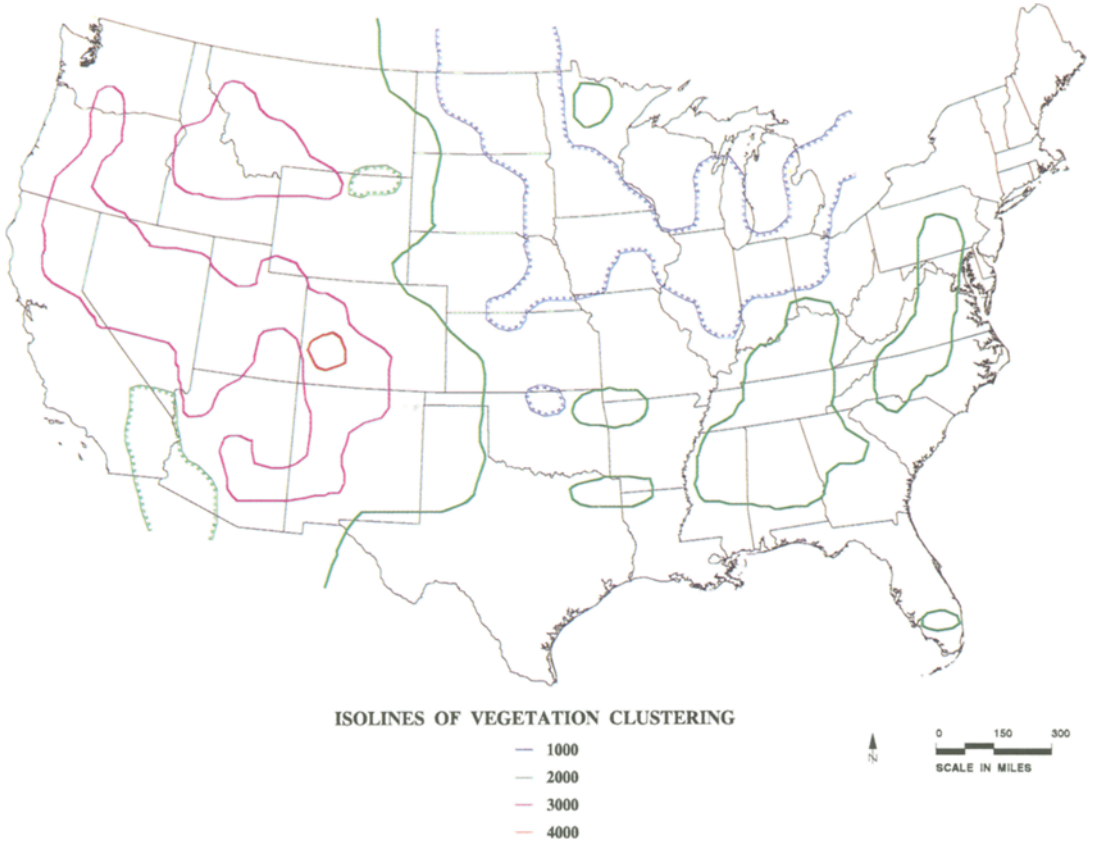

Fig. 6. Isoline map of vegetation clustering. Contour values are inclusive.

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