The Influence of Geomorphological Heterogeneity on Biodiversity
I. A Patch-Scale Perspective

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Abstract: Landscapes composed of spatially heterogeneous abiotic conditions should provide a greater diversity of potential niches for plants and animals than do homogeneous landscapes. We tested this hypothesis in a deciduous forest ecosystem in the northeastern United States. We created an index that summarizes the collective variation in terrain and soil properties in 2-ha study plots. We measured woody plant species richness and diversity in 20 study plots that had high geomorphological heterogeneity and 20 plots that had low geomorphological heterogeneity. The richness and diversity of trees and shrubs were significantly higher in sites with high geomorphological heterogeneity than in sites that exhibited little change in terrain or soil conditions. Variation in aspect and soil drainage were especially important predictors of biotic diversity. Our results demonstrate an intimate association between abiotic and biotic diversity and have significant implications for long-term conservation strategies.

Introduction

The science behind the development of strategies to protect endangered species has matured to the point that there is a widespread realization that communities, ecosystems, and landscapes must be the target of our efforts to conserve biodiversity (Noss 1983; Hunter et al. 1988; Franklin 1993; Scott et al. 1993; Kohn & Walsh 1994; Meilleur et al. 1994; Lombard 1995). There appears to be resounding agreement among ecologists and resource managers that the maintenance of biological diversity is a goal of paramount importance (Soulé 1986; Wilson & Peter 1988), yet the development of an efficient, comprehensive approach to the identification of biotically diverse landscapes has been elusive.
We present a technique to estimate relative biological diversity that utilizes geographic information system (GIS) technology (August et al. 1996) to estimate the collective variation in edaphic and topographic characteristics of specific regions of a landscape. The result is an index of geomorphological heterogeneity that quantifies spatial variation in abiotic conditions and that should be, we hypothesize, functionally related to biotic diversity.

Given the oft-cited linkage between biotic diversity and spatial heterogeneity (Huston 1994; Forman 1995; Rosenzweig 1995) and the specific proposition that geomorphologically variable landscapes should support diverse assemblages of plants and animals (Hunter et al. 1988; Samways 1990), we reasoned that geomorphological heterogeneity should be high in areas rich in biologic diversity and low in areas with meager biotas. The empirical test of this hypothesis was carried out within an eastern deciduous forest in Rhode Island (U.S.A.). Biotic diversity was compared to abiotic diversity in 40 2-ha plots for which we calculated indices of geomorphological heterogeneity and measured species richness and diversity of woody vascular plants.

Methods

Study Area

The study was conducted in the Biological Research Reserve of the University of Rhode Island W. Alton Jones Campus, West Greenwich, Rhode Island (41°38’N, 71°41’W). The research area contains over 400 ha of eastern deciduous forest, ranging from poorly drained hardwood swamps to oak and oak-pine stands on well-drained glacial till. Pine and oak occur on excessively drained glacial till. Pine and oak occur on excessively drained outwash deposits. The area has been protected from human disturbance for at least 70 years. Old stone walls suggest that past perturbations likely included cultivation and/or grazing. Known natural disturbances include a major fire that engulfed many of the ridges in 1942 and repeated gypsy moth (Lymantria dispar) defoliations in the early 1980s. No part of the research area contains primary forest. Major topographic features include two hills with steep slopes and a valley drained by a perennial stream. Elevation ranges from 60 m at the lower end of the valley to 146 m at the top of the hills. The valley contains steep sloped kames and eskers, flat outwash plains, and kettle holes, some of which contain water during the wet season (e.g., early spring).

Analysis of Geomorphology

Indices of geomorphological heterogeneity were computed for each of 234 2-ha cells that made up the study area and were based on digital representations of soils obtained from the Rhode Island Geographic Information System (RIGIS) database (August et al. 1995) and topography obtained from the 1:24,000 U.S. Geological Survey Digital Elevation Model (DEM) database (U.S. Geological Survey 1987; Maune 1996). Soil data were recompiled onto 1:15,840 orthophotos from the Soil Survey of Rhode Island (Rector 1981) and digitized into the GIS. Thirty-seven soil types (e.g., map units) occurred as 160 discrete areas (polygons) in the study area. Slope and aspect were derived from a triangular irregular network (TIN) model developed from the DEM. Soil depth consisted of five classes ranging from no true soil present to soils more than 82 cm deep. Slope was represented by five classes and ranged from less than 3.0% to more than 16.5%. Textures of the A and B horizons were each divided into seven classes, ranging from no soil present in the horizon to soils that were predominantly silt loams. Nine drainage classes were recognized, and these ranged from excessively drained soils to standing water. Aspect was divided into eight equal classes beginning with 0°N, with an additional class for level terrain. All GIS analyses were done by means of ARC/INFO software (Environmental Systems Research Institute, Redlands, California) on a Prime 9950 minicomputer and UNIX workstations.

Intracell variations in topographic aspect, slope, drainage, soil depth, and A and B horizon textures were estimated separately and in combination to produce an index of geomorphological heterogeneity for each 2-ha cell (Fig. 1). All six geomorphological features were combined into a single composite data set, and boundaries between adjacent polygons with identical geomorphological characteristics were eliminated (composite, Fig. 1). A grid of 2-ha cells was superimposed over the research area, creating 234 possible study plots. The Shannon-Weaver diversity index (\(H' = -\sum p_i \ln p_i\); Shannon & Weaver 1949) was used to create an index of geomorphological heterogeneity for each of the 234 cells. The proportional area (\(p_j\)) of every polygon exhibiting unique geomorphological properties within a cell was calculated and used to compute the diversity index for each cell. Cells with low variation in slope, aspect, drainage, soil depth, and texture generated low geomorphological heterogeneity values, whereas cells with many polygons of unique combinations of topographic and edaphic properties generated high geomorphological heterogeneity values.

Cells devoid of woody vegetation because of intensive management (e.g., hay fields) and water bodies were eliminated from the data set. Of the remaining cells, 20 each of the 30 most and 30 least diverse cells were selected randomly for plot establishment and subsequent vegetation analysis (Fig. 1). The 20 plots in which geomorphological heterogeneity was highest or lowest are referred to as “high geomorphological heterogeneity plots” and “low geomorphological heterogeneity plots,” respectively.
Analysis of Vegetation

Diversity of woody species and estimates of species dominance were determined in the 40 2-ha plots that represented the areas with the highest and lowest geomorphological heterogeneity (Fig. 1). Plots were delineated in the field in 1992 by standard surveying techniques from reference points that existed in the GIS database (e.g., trail intersections, hydrographic features). To offset potential minor inaccuracies in identifying plot boundaries, vegetation sampling was done inside a 12-m buffer zone within the perimeter of each plot.

In late summer and fall of 1992, the diversity and dominance of shrubs (woody perennials with a diameter at breast height (dbh) of less than 10.2 cm) and trees (woody perennials with a minimum dbh of 10.2 cm) were measured at 25 sample points within each 2-ha plot. Each point was positioned randomly within one of five equally spaced intervals along each of five transects in the interior of each plot. Each transect was oriented in a north-south direction, and each originated from a randomly located point within one of five equidistant intervals established along the north or south boundary of each plot. Species-area curves developed for shrub and tree species in a high geomorphological heterogeneity plot during a preliminary analysis indicated that a sample size of 25 points per plot was more than adequate to accurately portray the diversity of woody perennials in this eastern deciduous forest.

Shrub species richness and dominance were determined with the line-intercept technique (Canfield 1941). Data were collected from one 3-m intercept line positioned in a north-south direction at each of the 1000 points sampled. Dominance values for each species were measured as intercept coverage. Tree species richness and dominance were determined with the point-centered quarter method (Cottam & Curtis 1956). Dominance values for each species were measured as stem diameter at breast height. For both trees and shrubs, the “evenness” component of diversity was calculated from dominance.
data substituted into equations provided in Magurran (1988). These values were in turn substituted for $p_i$ in the Shannon-Weaver equation to create shrub and tree diversity indices for each plot.

**Statistical Analyses**

Data were tested to assess departures from a normal distribution with the Shapiro-Wilk Normality Test (Shapiro & Wilk 1965), and the $F_{max}$ statistic was used to detect heteroscedasticity (Sokal & Rohlf 1981). Coefficients of variation were used as estimates of the variability in shrub intercept coverage and tree diameter at breast height. The Student’s $t$ test and Wilcoxon rank sum test were used to compare measures of geomorphological heterogeneity between plots with high and low levels of biodiversity. A matrix of Spearman rank coefficients of correlation was computed to assess the interrelatedness of the six measures of geomorphological heterogeneity, and stepwise regression was used to determine the relative importance of the individual variables used to create our index of geomorphological heterogeneity. All statistical procedures were implemented with PC-SAS (SAS Institute, Cary, North Carolina) and Statistica (StatSoft, Inc., Tulsa, Oklahoma) software.

**Results**

Diversity in geomorphological features varied widely in an eastern deciduous forest in Rhode Island. The composite geomorphological heterogeneity index created for each 2-ha plot from data on aspect, drainage, soil depth, soil texture, and slope were significantly higher in the 20 plots with high geomorphological heterogeneity ($H' = 2.53$, SE = 0.04) than in the 20 plots with low geomorphological heterogeneity ($H' = 0.46$, SE = 0.06; $p < 0.001$).

The fundamental objective of this project was to determine whether or not measures of biological diversity would parallel the established differences in geomorphological heterogeneity between high and low geomorphological heterogeneity sites. The species richness of shrubs was significantly higher in high geomorphological heterogeneity plots (22.2 species, SE = 1.2) than in low geomorphological heterogeneity plots (12.0 species, SE = 0.8; $p < 0.001$; Fig. 2a). The species richness of trees was also significantly higher in high geomorphological heterogeneity plots (9.2 species, SE = 0.6) than in low geomorphological heterogeneity plots (5.8 species, SE = 0.4; $p < 0.001$).

Tree and shrub diversity differed significantly between low and high geomorphological heterogeneity plots ($p < 0.001$; Fig. 2b). Shrub and tree diversity were both higher in high geomorphological heterogeneity plots ($H' = 2.3$, SE = 0.06; $H' = 1.4$, SE = 0.08, respectively) than in low geomorphological heterogeneity plots ($H' = 1.6$, SE = 0.09; $H' = 1.0$, SE = 0.08, respectively).

Variability in vegetation structure differed significantly between plots with low and high geomorphological heterogeneity sites. The coefficients of variation of shrub coverage (based on intercept length) and tree diameter at breast height in plots with high and low geomorphological heterogeneity (c). In all cases $n = 20$ and mean values are bracketed by one standard error.
heterogeneity (Fig. 2c). The coefficient of variation in shrub canopy coverage was higher in high geomorphological heterogeneity plots (52.3%, SE = 2.8) than in low geomorphological heterogeneity plots (44.0%, SE = 2.3; \( p < 0.05 \)), and the coefficient of variation in tree diameter at breast height was higher in high geomorphological heterogeneity plots (52.8%, SE = 2.6) than in low geomorphological heterogeneity plots (31.5%, SE = 1.6; \( p < 0.001 \)).

We divided the analysis plots into those with species richness values larger than the median for shrub and tree species richness (high biodiversity) and those smaller than the median for species richness (low biodiversity; Table 1). All of the individual measures of geomorphological heterogeneity, except the diversity of texture in the A horizon of soils, were significantly greater in plots supporting high species richness of trees and shrubs.

A correlation matrix comparing all possible combinations of the six separate indices of geomorphological heterogeneity indicated that the six variables were significantly interrelated (\( p < 0.01 \)). There were differences, however, in the degree to which the six abiotic variables were related to the index of geomorphological heterogeneity. Topographic aspect accounted for more of the variation (partial \( r^2 = 0.94 \)) in the index of geomorphological heterogeneity than did any of the other five components of abiotic diversity used to generate this index. Soil texture diversities for the A and B horizons were the only abiotic variables that did not explain significant variation in our index of geomorphological heterogeneity; neither variable met the \( p = 0.15 \) inclusion limit of our stepwise regression model.

Aspect and drainage accounted for more of the variance in biotic richness and diversity than did any other abiotic variables. For example, aspect diversity accounted for the majority of all variance in shrub richness (partial \( r^2 \) for aspect = 0.55; total multivariate \( R^2 \) for all abiotic variables = 0.59). When aspect was removed from regression models, drainage accounted for the majority of the variance in all biotic variables except tree diversity.

**Discussion**

Convergent patterns of geomorphological heterogeneity and woody plant species diversity in an eastern deciduous forest provide evidence in support of the hypothesis that biotic diversity is a function, in part, of environmental diversity. Spatial heterogeneity is often cited as a factor that affects biotic diversity (August 1983; Huston 1994; Lapin & Barnes 1995; Rosenzweig 1995), yet to our knowledge there has been only one previous explicit test of this assumption in which multiple measures of landscape heterogeneity were compared to one or more components of biotic diversity (Harner & Harper 1976). Further, geomorphological parameters such as aspect and slope have long been known to influence vegetation (Cantlon 1953; Ayyad & Dix 1964; Killingbeck & Wali 1978; Forman 1995; Wu & Loucks 1995), but the specific influence of the spatial variability of these geomorphological parameters on species diversity has been addressed only once (Harner & Harper 1976).

For all combinations of plant type (shrubs and trees) and diversity (richness and diversity), plots characterized as having high geomorphological heterogeneity were the same plots that supported the highest plant diversities. Furthermore, variability in independent measures of species dominance was significantly higher in high geomorphological heterogeneity plots than in low geomorphological heterogeneity plots. Therefore, species richness, diversity, and dominance were all associated with spatial heterogeneity of abiotic properties.

We believe that differences in geomorphology within this eastern deciduous forest were the cause rather than

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**Table 1.** Mean (±1 SE) levels of diversity for each of the measures of geomorphological heterogeneity (GMH) and the composite index of GMH for analysis cells above (high) and below (low) the median value for shrub and tree species richness.\(^a\)

<table>
<thead>
<tr>
<th>Variable</th>
<th>Shrub species richness</th>
<th>Tree species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>high (( n = 20 ))</td>
<td>low (( n = 20 ))</td>
</tr>
<tr>
<td>Composite index</td>
<td>2.26 ± 0.15(^b)</td>
<td>0.73 ± 0.18</td>
</tr>
<tr>
<td>Aspect diversity</td>
<td>1.53 ± 0.08(^b)</td>
<td>0.48 ± 0.13</td>
</tr>
<tr>
<td>Drainage diversity</td>
<td>0.58 ± 0.09(^b)</td>
<td>0.09 ± 0.05</td>
</tr>
<tr>
<td>A horizon texture diversity</td>
<td>0.33 ± 0.08(^c)</td>
<td>0.08 ± 0.06</td>
</tr>
<tr>
<td>B horizon texture diversity</td>
<td>0.51 ± 0.08(^b)</td>
<td>0.08 ± 0.06</td>
</tr>
<tr>
<td>Slope diversity</td>
<td>1.12 ± 0.07(^b)</td>
<td>0.46 ± 0.09</td>
</tr>
<tr>
<td>Soil depth diversity</td>
<td>0.37 ± 0.08(^b)</td>
<td>0.08 ± 0.05</td>
</tr>
</tbody>
</table>

\(^a\)Probabilities are from the Wilcoxon rank sum statistic and test the hypothesis that geomorphological diversity is the same for sites characterized by high and low levels of biodiversity.

\(^b\)\( p < 0.001 \).

\(^c\)\( p < 0.05 \).

\(^d\)\( p < 0.01 \).
the effect of the observed patterns in plant diversity because the topographic and edaphic features used in our comparisons were primarily the result of nonbiological forces. For example, plants can be expected to have little if any effect on topographic aspect and slope. It is well known that abiotic environmental parameters such as soil temperature and available moisture may have reciprocal interactions with vegetation (Daubenmire 1959; Geiger 1966), yet such parameters were excluded from our analysis. Even the edaphic variables we used, with the possible exception of soil depth, had origins that were almost exclusively geological rather than biological. Therefore, it is reasonable to conclude that woody plant species diversity was a product of geomorphological heterogeneity in this eastern deciduous forest.

Although no attempt was made to correlate geomorphology with animal diversity, it is likely that geomorphological diversity is related to the diversity of all organisms, not just vascular plants (Wu & Loucks 1995). The reliance of many species of animals on species-specific plant resources indicates the high degree of interconnectivity between plant and animal diversity. Put simply, animal diversity "...is clearly due largely to the diversity provided by terrestrial plants" (Hutchinson 1959).

Of the organisms we studied, shrubs were somewhat more sensitive to geomorphological heterogeneity than trees. By virtue of the differences in their maximum sizes, these two forms of woody perennial plants react differently to environmental conditions (Carlile et al. 1989). The distribution, abundance, and diversity of the smaller, more numerous shrubs should more readily reflect small-scale deviations in microenvironmental variables. Because smaller plants have been found to be progressively more sensitive than larger plants to topographic variables, such as aspect (Cantlon 1953), it follows that our analysis is a conservative estimate of the strength of the relationship between the diversity of all plants and the GIS-derived index of geomorphological heterogeneity.

Among the six topographic and edaphic measures we used to estimate overall geomorphological diversity, all variables, except A-horizon soil texture class, were individually related to tree and shrub diversity. When all six variables were combined into a composite index of geomorphological heterogeneity, the vast majority of variance in plant richness and diversity was accounted for by aspect and drainage variation. Although soil drainage was an important correlate of biodiversity in our study area, the other edaphic and nonedaphic characteristics we measured may be equally or more important than drainage diversity at other sites. Furthermore, abiotic variables not measured here may also be instrumental in successfully predicting biotic diversity; this possibility should be explored. Nevertheless, the consistent effectiveness of aspect and drainage in predicting biotic diversity is indicative of both the strength of the fundamental relationship between these abiotic variables and biotic diversity and the efficacy of using them to predict relative levels of biotic diversity (Burnett 1995).

The degree to which our technique can be applied universally is not yet known. A significant link between the spatial heterogeneity of abiotic characteristics and plant species diversity in pinyon-juniper ecosystems (Harner & Harper 1976) suggests that the relationship between abiotic and biotic diversity is not restricted to eastern deciduous communities, yet many general questions about this relationship remain unanswered. For example, we need to know if indices of geomorphological heterogeneity predict relative levels of biotic diversity in sites that are (1) widely variable in total area covered, (2) dominated by community types other than eastern deciduous forest or pinyon-juniper shrubland, (3) dominated by a wide spectrum of community types, and/or (4) divergent in their disturbance histories. Site size (Johnson & Raven 1973; Rosenzweig 1995), community type (Fisher 1960; MacArthur 1972), and disturbance history (Armesto & Pickett 1985; Petraitis et al. 1989; Hobbs & Huenneke 1992) all play pivotal roles in determining plant distribution and diversity, yet our analysis took place in relatively small plots of equal size that were dominated by eastern deciduous forest and that had similar recent disturbance histories. Encouraging results from a test of this technique in large, discontinuous sites dominated by a wide variety of community types (Nichols et al. 1998) supports the tenet that regions of high geomorphological heterogeneity support more diverse biotic communities than are found in nearby regions of low geomorphological heterogeneity.

Conclusions

The coupling of biotic and abiotic landscape traits that we observed in a Rhode Island forest enabled us to use simple edaphic and topographic variables to predict the relative richness and diversity of woody plant species. Areas inherently high in geomorphological heterogeneity supported woody floras richer and more diverse than those of areas of low geomorphological heterogeneity. The ramifications of these findings are clearly significant with respect to ecological theory, but their implications with regard to the conservation of biological resources are equally important.

The supposition that biotic diversity is ecologically and aesthetically valuable has prompted conservation agencies and governments to suggest that protection be afforded to landscape parcels that are biologically diverse. There appears to be ecological merit in this strategy (Naeem et al. 1994), but measuring levels of biological richness and diversity is often a costly, time-consuming process (Burbidge 1991). Our technique of estimating...
relative biological diversity by examining variation in geomorphological properties based on easily obtained GIS databases offers an alternative to the time-consuming task of orchestrating field studies to prepare species checklists for multiple landscape parcels. The presence or absence of specific species cannot be definitively ascertained with our protocol, yet it should be possible to use the technique to identify probable locations of such species once their habitat requirements are known in detail (Clark et al. 1993; Cherrill et al. 1995; Sperduto & Congalton 1996). It is also true that protection of regions of high species richness is not always the goal of conservation agendas. When the focus of a conservation strategy is protection of endemic taxa, umbrella species, or keystone organisms (Wilcox 1984; Lombard et al. 1995; Kiester et al. 1996; Berger 1997), our protocol will have limited value. But in instances when relative estimates of biological richness are required, use of our method can increase the efficiency of field surveys by targeting areas of high potential diversity. Predicting potential patterns of species diversity in landscapes that have been denuded or subjected to severe disturbance is also a feasible application of our assessment strategy.

Our method of quantifying geomorphological heterogeneity should be broadly applicable to most landforms and geographic regions, but the specific components of GMH that are most relevant will assuredly vary geographically. For example, variation in terrain variables, such as slope and aspect, at the scale of our analysis (±3 m vertical resolution) is of little significance in plains or savanna habitats where topography varies little. Furthermore, the availability of digital representation of basic geomorphological data, such as soils, geology, and terrain, varies considerably across regions and among countries.

In the past few years there has been a strong emphasis on ecosystem or landscape-level conservation strategies (Noss 1983; Hunter et al. 1988; Franklin 1993; Kohn & Walsh 1994; Meilleur et al. 1994; Grumbine 1997). Protection of landscapes based on the existence of specific species has obvious short-term benefits, but long-term changes in the environment (e.g., climatic changes) render specific species assemblages transient, not static. Hunter et al. (1988) and Samways (1990) have recognized that landscapes of high geomorphological heterogeneity have probably supported diverse biotic communities in the past and will do so in the future, even though the species composition of these communities will invariably change over time. They argue that protection of regions with unique geomorphological properties is a desirable long-term conservation goal because these regions will always support unique biota. The protocol we offer here provides a mechanism with which to identify areas of high geomorphological heterogeneity, and our data on plant diversity and richness are consistent with the ideas of Hunter et al. (1988): sites with high geomorphological heterogeneity support a diverse flora of woody plants.

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Literature Cited


