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The Influence of Geomorphological Heterogeneity on Biodiversity

II. A Landscape Perspective

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Abstract: *The influence of geomorphological heterogeneity on vascular plant species richness was studied in 26 Rhode Island Audubon refuges ranging in size from 1.4 to 58.6 ha. Indices of abiotic heterogeneity reflecting spatial variation in slope, aspect, and soil drainage were calculated from extant databases in a geographic information system. After removing the influence of refuge size on both biotic diversity and geomorphological heterogeneity, vascular plant species richness was found to be highly related to geomorphological heterogeneity. Diversity in soil drainage class alone accounted for more than 50% of the variance in total plant species richness ($r^2 = 0.53$, $p < 0.001$) and was significantly related to the species richness of 10 of the 11 life-form classes of plants studied. When two refuges considered to be mathematical and biological outliers were removed from the regression analysis, soil drainage heterogeneity accounted for more than 65% of the variance in total plant species richness ($r^2 = 0.67$, $p < 0.001$). Aspect heterogeneity, slope heterogeneity, and the composite index of all three measures of geomorphological heterogeneity were each less related to total plant richness than soil drainage heterogeneity alone, but they were all more effective at predicting richness of native woody species ($r^2 = 0.23$-0.45, $p < 0.05$) than soil drainage heterogeneity ($r^2 = 0.08$, $p > 0.05$). In a stepwise multiple regression analysis, soil drainage heterogeneity and refuge size explained 66% ($p < 0.001$) of the variation in species richness (soil drainage heterogeneity, partial $r^2 = 0.39$; refuge size, partial $r^2 = 0.27$). These results explicitly support the tenet that geomorphological heterogeneity plays a major role in determining species richness. Because biotic and abiotic diversity were intricately linked at the scale of the landscape, conservation of geomorphological heterogeneity may be an effective strategy for conserving biodiversity.*

Influencia de la Heterogeneidad Geomorfológica en la Biodiversidad II. Una Perspectiva de Paisaje

Resumen: *La influencia de la heterogeneidad geomorfológica en la riqueza de especies de plantas vasculares se estudió en 26 refugios de Rhode Island Audubon que variaron en tamaño de 1.4 a 58.6 ha. Se estimaron índices de heterogeneidad abiótica reflejantes de una variación espacial en pendiente, aspecto y drenaje del suelo a partir de bases de datos de Sistemas de Información Geográfica. Una vez removida la influencia del tamaño del refugio tanto para la diversidad biótica, como para la heterogeneidad geomorfológica, la riqueza de plantas vasculares se encontró altamente relacionada con la heterogeneidad geomorfológica. Tan solo la diversidad en las clases de drenaje del suelo explicó 50% de la variabilidad en la riqueza total de especies de plantas ($r^2 = 0.53$, $p < 0.001$) y estuvo significativamente relacionada con la riqueza de plantas en 10 de las 11 clases de plantas estudiadas. Cuando dos refugios considerados matematica y biológicamente casos extremos fueron removidos del análisis de regresión, la heterogeneidad del drenaje del suelo explicó mas del 65% de la varianza de la riqueza total de plantas ($r^2 = 0.67$, $p < 0.001$). La heterogeneidad del aspecto, la heterogeneidad de la pendiente y el índice de composición de las tres mediciones de heterogeneidad geomorfológica estuvieron menos relacionadas con la riqueza total de plantas que la heterogeneidad del drenaje del suelo sola, pero fueron en conjunto mas efectivas para predecir la riqueza de las especies nativas de maderas ($r^2 = 0.23$, $p < 0.05$) que la heterogeneidad del drenaje del suelo ($r^2 = 0.08$, $p > 0.05$). En un análisis de regresión múltiple por pasos, la heterogeneidad del drenaje del suelo y el tamaño del refugio explicaron 66%*

(p < 0.001) de la variación de la riqueza de especies (heterogeneidad del drenaje del suelo, r^2 parcial $= 0.39$; tamaño del refugio, r^2 parcial $= 0.27$). Estos resultados soportan explícitamente el principio de que la heterogeneidad geomorfológica juega un papel significativo en la determinación de la riqueza de especies. Debido a que la diversidad biótica y abiótica estuvieron ligados de manera intrincada a escala de paisaje, la conservación de la heterogeneidad geomorfológica puede ser una estrategia efectiva para la conservación de la biodiversidad.

Introduction

Plant species richness was recently found to be highly related to four measures of geomorphological heterogeneity in plots of equal size within an eastern deciduous forest (Burnett 1995; Burnett et al. 1998). We successfully isolated the specific effects of geomorphological heterogeneity on biodiversity at the patch scale in this study by using a geographic information system (GIS) to formulate indices of geomorphological heterogeneity from extant datasets. It is not yet clear, however, if geomorphological heterogeneity can be used successfully to predict biodiversity at the landscape scale. For example, are geomorphological heterogeneity and biodiversity intricately interrelated in large, discontinuous sites that support a wide variety of community types?

Interest in the development of a technique to predict biodiversity from geomorphological heterogeneity has emerged from the recent realizations that (1) biodiversity is being diminished at an extremely rapid rate (Ehrlich & Wilson 1991; Soulé 1991; Groombridge 1992), (2) ecosystem functions can be altered or impaired by a loss of biodiversity (May 1977; Pimm 1984; Naeem et al. 1994; Tilman & Downing 1994), and (3) biodiversity may best be conserved by preserving unique and diverse physical environments that, unlike biological communities, are not merely transitory on a geological time scale (Hunter et al. 1988). Our primary goal was to determine the degree to which geomorphological heterogeneity can be used to predict vascular plant species richness at the landscape level. Additional objectives included an examination of the effects of area, disturbance, and vascular plant life form on the relationship between plant diversity and geomorphological heterogeneity, and an evaluation of the proposition that preserving landscapes high in geomorphological heterogeneity constitutes an effective strategy for conserving biodiversity.

Methods

Analysis of Plant Species Diversity

Complete lists of vascular plant species for 26 refuges of the Audubon Society of Rhode Island (ASRI) (41° 54'–41° 09' latitude and 71° 45'–71° 12' longitude) were used as the measure of biodiversity in this study. Lists were prepared from field surveys conducted throughout the 1993 and 1994 growing seasons. Sixteen plant communities dominated these refuges (Table 1). These communities represent most major plant associations in Rhode Island and are remarkably diverse in biological form and ecological function (i.e., grass-dominated salt marshes and dunes, shrub-dominated wetlands, and tree-dominated forests). The 26 refuges ranged in size from 1.4 to 58.6 ha (Table 2) and were distributed throughout the state (Fig. 1).

Table 1. Plant communities present in the 26 Rhode Island refuges.

Refuge	A	B	C	D	E	F	G	H	M	O	P	Q	R	S	W	Z
Beech Grove								X								
Brown Ravine								X			X					
Cocumscussoc				X				X			X		X			
Conant		X														
Davis			X		X		X					X	X			
Donovan								X			X					
Fox Hill	X							X			X					
Gould Island								X								
Indian Run Woods								X				X				
Kimball						X						X	X			
Lafayette	X							X				X				
Lewis Dickens	X			X	X				X							
Marsh Meadows	X								X							
Ocean Drive	X		X					X								
Otter Point												X			X	
Perched Boulder											X	X				
Powder Mill Ledges					X		X			X	X	X	X		X	
Ram Island	X							X		X						
Robinson Knight								X				X				
Ruecker	X							X	X	X		X				
South Branch	X								X				X	X		
Seavey								X				X				
Shadblow	X							X				X				
Stearns								X				X				
Touisset Marsh	X		X					X			X	X				
Usher Cove	X							X	X			X				

*A, Atlantic white cedar swamp (Chamaecyparis thyoides (L.)); B, black cherry and shadbush woodland (Prunus serotina Ehrh. and Amelanchier canadensis (L.), respectively); C, coastal dune; D, dwarf shrub bog; E, emergent marsh; F, oak-pine forest; G, sandplain grassland; H, mixed hardwood forest; M, salt marsh; O, old field; P, pastureland; Q, oak forest (Quercus); R, red maple swamp (Acer rubrum L.); S, shrub wetland; W, white pine forest (Pinus strobus L.); Z, aquatic plant bed.

Table 2.   Vascular plant species richness in the 26 Rhode Island refuges.*

Refuge	Spp	Area	SD	H	S	T	N	NN
Beech Grove	172	4.3	40	111	46	15	123	49
Brown Ravine	148	2.8	53	92	34	22	105	43
Cocumscussoc	168	4.8	35	107	39	22	143	25
Conant	56	1.4	41	51	5	0	29	27
Davis	314	21.5	15	215	70	29	236	78
Donovan	186	1.9	100	133	41	12	142	44
Fox Hill	237	20.0	12	195	34	8	152	85
Gould Island	124	2.7	46	78	31	15	73	51
Indian Run Woods	202	26.3	8	138	47	17	152	50
Kimball	194	12.0	16	123	50	21	150	44
Lafayette	171	6.5	27	112	35	24	148	23
Lewis Dickens	216	58.6	4	174	34	8	144	72
Marsh Meadows	166	12.6	13	120	36	10	122	44
Ocean Drive	132	3.9	34	99	28	5	79	53
Otter Point	205	4.4	46	135	47	23	172	33
Perched Boulder	192	22.9	8	131	40	21	179	13
Powder Mill Ledges	455	34.9	13	331	77	47	341	114
Ram Island	146	8.4	17	102	35	9	119	27
Robinson Knight	198	22.1	9	135	41	22	164	34
Ruecker	432	24.5	18	318	73	41	286	146
South Branch	285	6.7	43	210	55	20	219	66
Seavey	112	5.9	19	65	29	18	110	2
Shadblow	180	11.2	16	126	41	13	150	30
Stearns	143	12.3	12	91	32	20	122	21
Touisset Marsh	360	24.9	14	286	45	29	237	123
Usher Cove	284	4.7	61	210	48	26	183	101

**Spp*, total species; Area, refuge area in ha; SD, species density in species per hectare; H, herb species; S, shrub species, including all species of vines; T, tree species; N, native species; NN, nonnative species.*

Figure 1.   Locations and names of the 26 Rhode Island refuges used in this study.

Analysis of Geomorphological Heterogeneity

Audubon Society of Rhode Island refuge boundaries were digitized in a geographic information system (GIS) using ARC/INFO 7.1 software (Environmental Systems Research Institute, Redlands, California) on a Data General 5220 Unix Workstation. Soil maps were digitized from the *Soil Survey of Rhode Island* (Rector 1981) to provide soil drainage information. A triangular, irregular network (TIN) model, developed from 1:24,000 digital elevation models (U.S. Geological Survey 1987; Maune 1996), was used to derive slope and aspect information. For each ASRI refuge, GIS overlay procedures created coverages for slope, aspect, soil drainage, and a composite utilizing all three geomorphological characteristics.

Fourteen classes of soil drainage, varying from excessively drained to water bodies, were found among the 26 refuges. Classes of aspect were north (N), northeast (NE), east (E), southeast (SE), south (S), southwest (SW), west (W), northwest (NW), and SLOPE <3% for level terrain where the biological significance of aspect is minimal. Slope classes were <3.00%, 3.00–8.49%, 8.50–12.49%, 12.50–16.49%, and ≥16.5%.
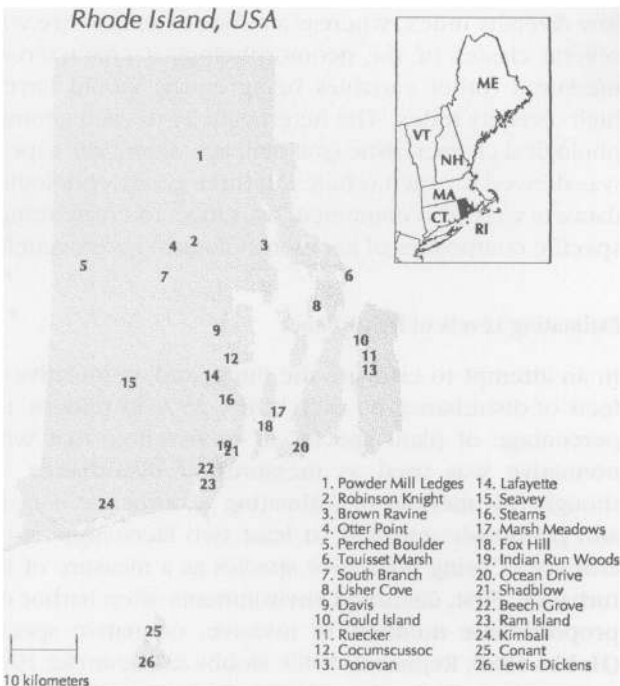
Ideally, the number of classes into which each measure of geomorphological heterogeneity is divided should be equal, but drainage was divided into more classes (14) than aspect (9) or slope (5). Although this was a function of the fact that more drainage classes were present in the 26 refuges than the standard number of aspect (e.g., N, NE, etc.) or slope divisions, this could have influenced the relative contributions of each measure of geomorphology to the prediction of biotic diversity. If such an inequality in geomorphology classes was of paramount importance in our analyses, then drainage would have influenced the composite index more than aspect or slope. But the composite index of geomorphological heterogeneity was not significantly correlated with the drainage heterogeneity index ($r = 0.35$, $p > 0.05$). Conversely, the indices of slope and aspect heterogeneity were both highly correlated with the composite index of geomorphological heterogeneity ($r = 0.78$, $p < 0.001$; $r = 0.88$, $p < 0.001$, respectively).

Indices of geomorphological heterogeneity were calculated with the Shannon-Weaver index (Shannon & Weaver 1949) applied to our geomorphological data. For example, the index of soil drainage heterogeneity (H') for a refuge was derived from the sum of the $p_i log$ p_i value for each soil drainage class, where p_i is the proportion of the total area of the refuge occupied by soil drainage class i. A refuge with little variation in the geomorphological characteristic measured would have a

low diversity index, whereas a refuge of similar size with several classes of the geomorphological characteristic measured (other variables being equal) would have a high diversity index. The heterogeneity of each geomorphological characteristic (soil drainage, slope, and aspect) was derived for each refuge. All three geomorphological datasets were also combined, by refuge, to create refuge-specific composites of geomorphological heterogeneity.

Estimating Levels of Disturbance

In an attempt to estimate the integrated, cumulative effects of disturbance on each of the 26 ASRI refuges, the percentage of plant species in each refuge that were nonnative was used as measures of disturbance. Although this method of estimating disturbance is novel and previously untested, at least two facts support the efficacy of using nonnative species as a measure of disturbance. First, disturbed environments often harbor disproportionate numbers of invasive, nonnative species (Hobbs 1989; Rejmanek 1989; Hobbs & Huenneke 1992; Rejmanek & Richardson 1996). Therefore, landscapes that support a high percentage of nonnative species have been subjected to high levels of disturbance. Second, the observed relationship between biodiversity and percentage of nonnative species in the ASRI refuges—species richness peaked in refuges with intermediate percentages of nonnative species—was identical to the general relationship between biodiversity and disturbance predicted by the intermediate disturbance hypothesis of Connell (1978).

Statistical Analyses

Geographic area is intricately related to species richness over a wide range of spatial scales (MacArthur & Wilson 1967; Huston 1994; Rosenzweig 1995). To eliminate area as a confounding factor, we used residuals from a linear regression comparing refuge area to vascular plant species richness as the measure of biodiversity for each refuge. Ecologically, these residuals represented the unexplained variability in species richness after the effect of refuge size was removed. Mathematically, the residual for each refuge is the distance between the regression line and the x,y coordinate of that refuge in the regression.

Although it was not strictly necessary to remove the effects of refuge size on indices of geomorphological heterogeneity because refuge size was not significantly correlated with slope heterogeneity, aspect heterogeneity, or soil drainage heterogeneity (r = 0.30, 0.21, and 0.12, respectively; Spearman rank correlation; p > 0.05), we did so because geomorphological heterogeneity would be expected a priori to be positively associated with area (M. Huston, personal communication). Therefore, residuals from four linear regressions comparing refuge area to each of the four measures of geo-

morphological heterogeneity were used as measures of geomorphological heterogeneity. Linear regression analyses were used to compare the measures of geomorphological heterogeneity (independent variables) with species richness (dependent variable), and with refuge size itself (dependent variable).

Stepwise multiple regression was used to determine the coefficient of determination of species richness from three variables: soil drainage heterogeneity, disturbance (measured as the percentage of species in each refuge that were nonnative), and refuge size. Because refuge size was one of the variables compared to plant species richness in this multiple regression analysis, area (i.e., refuge size) was not factored out of the plant species richness data as it was previously through the use of residuals. The degree to which geomorphological indices (soil drainage, slope, aspect, and the composite) were related to one another was estimated with the Spearman rank correlation statistic. PC-SAS (SAS Institute, Cary, North Carolina) and Statistica (StatSoft Inc., Tulsa, Oklahoma) software were used for all statistical analyses.

Results

We identified 869 vascular plant species in the 26 refuges. This represents approximately 50% of the entire vascular flora of Rhode Island (Palmatier 1952; George 1996). Twenty-eight percent of the species growing in the 26 refuges were nonnative. Proportions among life forms were 78% herbs, 14% shrubs, and 8% trees. Plant richness varied from 56 species in Conant Refuge to 455 species in Powder Mill Ledges Refuge. Plant species density ranged from 4 species/ha in Lewis Dickens Refuge to 100 species/ha in Donovan Refuge (Table 2).

Biotic and geomorphological heterogeneity were intricately linked at the scale of the landscape (Table 3). Among the four measures of geomorphological heterogeneity, soil drainage was the best predictor of total vascular plant richness in all 26 refuges (r^2 = 0.53, p < 0.001; Fig. 2). Two refuges, however, supported abnormally high and low numbers of vascular plant species (Fig. 2), presumably because of intense land management. Abnormally high species richness has been maintained in the Powder Mill Ledges Refuge because of the existence of a complex mosaic of asynchronously disturbed landscape patches, including power line and gas line right-of-ways. Abnormally low species richness has been maintained in the Lewis Dickens Refuge because of the combined effects of cattle grazing and a management plan designed to minimize woody plant species. When data from these two refuges were removed from our regression analyses, soil drainage heterogeneity accounted for more than 65% of the variance in vascular plant species richness (r^2 = 0.67, p < 0.001, n = 24).

Even though data from these two refuges could have been permanently removed from our analyses on the grounds that they were mathematical and ecological outliers, we chose to retain these data in all analyses except the single regression listed above. We believe that this conservative approach preserves the generality of our analysis.

Soil drainage heterogeneity accounted for more of the variance in the richness of herbs ($r^2 = 0.53, p < 0.001$), shrubs ($r^2 = 0.31, p < 0.01$), native plants ($r^2 = 0.33, p < 0.01$), nonnative plants ($r^2 = 0.43, p < 0.001$), native herbs ($r^2 = 0.39, p < 0.001$), nonnative herbs ($r^2 = 0.36, p < 0.001$), and nonnative woody plants ($r^2 = 0.41, p < 0.001$) than any other measure of geomorphological heterogeneity. Soil drainage heterogeneity had a significant impact on the richness of every class and life form of plant studied except native woody plants (Table 3). However, the magnitude and significance of the relationship decreased along a life-form gradient from herbs ($r^2 = 0.53, p < 0.001$) to shrubs ($r^2 = 0.31, p < 0.01$) to trees ($r^2 = 0.18, p < 0.05$).

Slope and/or aspect heterogeneity were significantly related to the species richness of trees (slope $r^2 = 0.21, p < 0.05$) and native woody plants (aspect $r^2 = 0.23, p < 0.05$; slope $r^2 = 0.27, p < 0.01$), yet coefficients of determination between slope and aspect heterogeneity and all other classes of plants were low (Table 3). The composite index of geomorphological heterogeneity
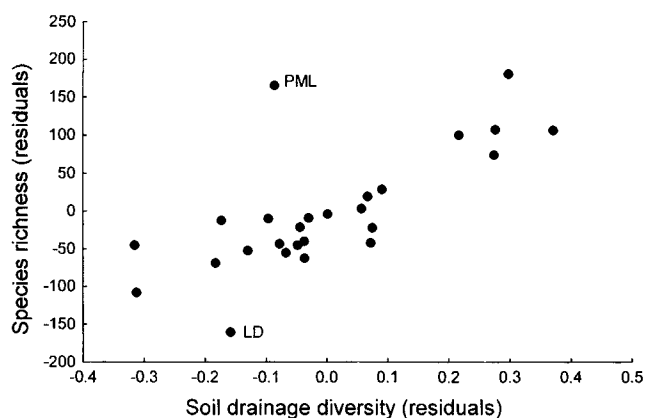

Figure 2. Relationship between residuals of soil drainage heterogeneity and residuals of vascular plant species richness in the 26 Rhode Island refuges ($r^2 = 0.53$; p < 0.001). Residuals represent the variability in heterogeneity and species richness that remained unexplained after the effects of refuge size were removed with linear regression. More than 65% of the variance in plant species richness was accounted for by soil drainage heterogeneity when Powder Mill Ledges Refuge (PML) and Lewis Dickens Refuge (LD) were removed from the dataset ($r^2 = 0.67$; p < 0.001; n $= 24$).

was a better predictor of tree species richness ($r^2 = 0.41, p < 0.001$) and native woody plant richness ($r^2 = 0.45, p < 0.001$) than any other measure of geomorphological heterogeneity. The composite geomorphological heterogeneity index was also a significant predictor of woody plant richness ($r^2 = 0.25, p < 0.01$) and native plant richness ($r^2 = 0.20, p < 0.05$).

Refuge size was significantly related to species richness in all classes of native plants (Table 3; all native plants, $r^2 = 0.42, p < 0.001$; native herbs, $r^2 = 0.43, p < 0.001$; native woody species, $r^2 = 0.21, p < 0.05$). Refuge size was also significantly related to total species richness ($r^2 = 0.41, p < 0.001$), herb richness ($r^2 = 0.43, p < 0.001$), and shrub richness ($r^2 = 0.17, p < 0.05$). The coefficient of determination describing the degree of relatedness between refuge size and species richness of "all native plants" was higher than the coefficients relating each of four measures of geomorphological heterogeneity to native plant richness. Refuge size was not significantly related to any of the three classes of nonnative plants.

The 26 ASRI refuges varied widely in the number and percentage of nonnative species they supported (Table 2). The percentage of nonnative species growing in individual refuges was used as a measure of disturbance and varied from less than 2% in Seavey Refuge to 48% in Conant Refuge. Soil drainage heterogeneity, refuge size, and

Table 3. Coefficients of determination derived from comparisons of geomorphological heterogeneity and refuge size with vascular plant species richness in 26 Rhode Island refuges.[a]

Class of plants	Geomorphological variables				Refuge size
	Drainage	Aspect	Slope	Composite	
	...............heterogeneity...................				
All plants	0.53[b]	0.02	0.04	0.11	0.41[b]
All herbs	0.53[b]	0.00	0.01	0.04	0.43[b]
All shrubs	0.31[c]	0.04	0.05	0.13	0.17[d]
All trees	0.18[d]	0.13	0.21[d]	0.41[b]	0.10
All woody	0.28[c]	0.09	0.09	0.25[c]	0.14
All native	0.33[c]	0.03	0.11	0.20[d]	0.42[b]
All nonnative	0.43[b]	0.05	0.03	0.01	0.11
Native herbs	0.39[b]	0.00	0.07	0.12	0.43[b]
Native woody	0.08	0.23[d]	0.27[c]	0.45[b]	0.21[d]
Nonnative herbs	0.36[b]	0.10	0.05	0.03	0.13
Nonnative woody	0.41[b]	0.00	0.00	0.01	0.05

[a] *Residuals of the four measures of geomorphological heterogeneity were compared to residuals of plant species richness. Residuals represent the variability in geomorphological heterogeneity and plant species richness that remained unexplained after the effect of refuge size was removed. Refuge size was compared directly to plant species richness.*
[b] p < 0.001.
[c] p < 0.01.
[d] p < 0.05.

disturbance collectively accounted for 66% of the total variation in plant species richness (multivariate R^2 = 0.66; p < 0.001; stepwise multiple regression). Soil drainage heterogeneity accounted for the majority of the variance in plant species richness (partial r^2 = 0.39, p < 0.001). Refuge size accounted for the next highest amount of variance (partial r^2 = 0.27, p < 0.001), and disturbance was completely eliminated from the regression equation because it did not meet the minimum significance threshold required to enter the model (p = 0.15).

Discussion

Geomorphological Heterogeneity

Theoretical explorations of the relationship between biotic and abiotic diversity are abundant (Groombridge 1992; Huston 1994; Rosenzweig 1995), and all three of the individual geomorphological variables analyzed in this study have been previously related to community structure and composition. Moisture availability has often been shown to affect plant distribution and abundance in developing plant communities (Heinselman 1970; Gosselink & Turner 1978; Holland & Burk 1990), thus indicating the importance of soil drainage. The influence of slope and aspect on plant community structure has also been well documented (Shreve 1924; Cantlon 1953; Ayyad & Dix 1964; Hutchins et al. 1976).

Few studies, however, have directly linked empirical measures of geomorphological heterogeneity to plant species richness or diversity. Harner and Harper (1976) compared geomorphological heterogeneity to plant diversity in relatively undisturbed or equally disturbed pinyon-juniper ecosystems in Utah and New Mexico. Plant species diversity was found to be highly related to both area (partial r^2 = 0.92) and an index of geomorphological heterogeneity based on variation in eight environmental parameters (partial r^2 = 0.79). Area and geomorphological heterogeneity combined explained over 98% of the variation in species diversity. Burnett et al. (1998) compared geomorphological heterogeneity to the richness and diversity of woody plant species in 2-ha plots within an eastern deciduous forest in Rhode Island. Six topographic and edaphic variables were combined into geomorphological diversity indices that accounted for 50–60% of the total variation in overstory woody plant diversity. These same indices were also related to measures of variability in species abundance (Burnett et al. 1998).

What has not been clear, however, is whether the results from single-community-type studies can be applied more broadly to highly diverse landscapes. Specifically, are geomorphological heterogeneity and biotic diversity highly related in landscape patches that are geographi-

cally separate, variable in total size, and dominated by a wide array of plant community types?

Geomorphological heterogeneity was intricately linked to vascular plant species diversity in 26 ASRI refuges that varied widely in size and community composition. This linkage supports the hypothesis that spatial heterogeneity plays a pivotal role in determining species diversity, and it indicates the efficiency and widespread applicability of the GIS-based technique used in this study to predict vascular plant species richness in landscape parcels that vary in size and community composition.

Of all the measures of geomorphological heterogeneity examined, soil drainage heterogeneity was the best overall predictor of plant richness. It explained 53% of the variation in total species richness of all refuges and 67% of the variation in the 24 refuges that were not routinely subjected to intensive management practices. Further, soil drainage heterogeneity was a significant predictor of species richness in 10 of the 11 classes of plants studied. This corroborates the importance of water availability to the abundance and distribution of plant species, but it goes well beyond this general maxim to suggest that the heterogeneity of water availability within a landscape is highly related to the number of species that landscape can support.

The ability of soil drainage heterogeneity to predict species richness among plant life-form classes increased from trees to shrubs to herbs. The influence of aspect on plant species composition also increased along a continuum from trees to shrubs to herbs on Cushetunk Mountain in New Jersey (Cantlon 1953). Plants with high biomass and long life spans are generally better buffered against changes in the environment than small plants with short life spans (Cantlon 1953; Grime 1979). As abundance and species diversity increase as life form size decreases, the ability of plants to differentiate between more subtle environmental gradients may increase. This general pattern suggests that the species richness of small plants is more sensitive to soil drainage heterogeneity than is the species richness of large woody perennials.

On the contrary, it was the woody species that were more sensitive to aspect and slope heterogeneity than the smaller herb species. This pattern also held for the composite index of geomorphological heterogeneity, primarily because slope and aspect heterogeneity controlled the behavior of the composite index. On each of the 26 refuges there were substantially fewer areas of unique soil drainage classes than areas of unique slope and aspect classes. This, in addition to the generally weaker association between slope and aspect with biodiversity in this study (compared with soil drainage heterogeneity), caused the composite index of all three geomorphological measures to be less effective than soil drainage heterogeneity alone in predicting total species richness.

The utility of predicting biodiversity from indices of geomorphological heterogeneity is particularly appealing from a pragmatic standpoint. First, sharp increases in the cost of conducting biological field surveys have intensified the need for developing cost-effective alternatives (Burbidge 1991). By reducing the need for extensive field studies used traditionally to document levels of biodiversity, our technique can considerably enhance the efficiency and reduce the costs of biodiversity assessments. Second, the time needed to predict levels of biodiversity with this technique is but a fraction of the time needed to design and implement field studies that would directly measure biodiversity. Therefore, prediction of biodiversity from measures of geomorphological heterogeneity appears to be a cost-effective, time-efficient means of identifying regions of landscape that likely support a rich biota.

Refuge Size

Geographic area is known to influence species diversity (MacArthur & Wilson 1967; Johnson & Raven 1973; Rey 1981; Huston 1994; Rosenzweig 1995), but teasing apart the effects of area from those of geomorphological heterogeneity has been difficult. To eliminate area as a confounding factor in our assessment of how geomorphological heterogeneity affects biodiversity, we used linear regression residuals as measures of the unexplained variability in species richness after the effect of refuge size was removed.

Area accounted for a significant fraction of the variance in species richness in all classes of native plants in the 26 ASRI refuges. Area was not, however, significantly related to the richness of nonnative species. The apparent inability of area to predict the richness of nonnative species is likely the result of disturbance, which may temporarily preempt the influence of area on biotic diversity. Nonnative species are abundant in disturbed environments (Denslow 1980; Hobbs 1989; Rejmanek 1989; Hobbs & Huenneke 1992), and disturbance confuses the species-area relationship by increasing the importance of physiological tolerances to stress (Denslow 1980) while potentially decreasing the overall influence of geomorphological heterogeneity.

As important as area is to determining plant richness in most environments, geomorphological heterogeneity proved to be more important than area in predicting species richness in the 26 ASRI refuges. Soil drainage heterogeneity exerted a greater effect on total plant species richness than area (Table 3), thus allowing it to be used as a more precise independent predictor of biodiversity. Aspects of geomorphology are more directly correlated with species diversity than area itself in other studies (Koopman 1958; MacArthur 1964; Power 1972; Johnson 1975).

Relative and Combined Effects of Soil Drainage Diversity, Refuge Size, and Disturbance

The fact that soil drainage heterogeneity explained more variation in plant species richness (partial $r^2 = 0.39$, $p < 0.001$) than either refuge size (partial $r^2 = 0.27$, $p < 0.001$) or disturbance ($p > 0.15$) underscores the importance of geomorphological heterogeneity—specifically, soil drainage heterogeneity—as a determinant of plant species richness. Further, this observed relationship supports the tenet that geomorphological heterogeneity can be used effectively to predict at least some aspects of biodiversity.

Because disturbance plays an important role in determining plant diversity (Denslow 1980; Armesto & Pickett 1985; Petraitis et al. 1989; Hobbs & Huenneke 1992; Reice 1994), its minimal impact on our stepwise regression model was initially somewhat surprising. There appear, however, to be several explanations for this weak relationship. First, because disturbance alters plant diversity both positively and negatively (Pickett & White 1985; Rosenzweig 1995), it is possible that the concomitant enrichment and diminution of plant species due to the variable effects of disturbance offset each other in our multisite analysis. Second, disturbance may simply have a relatively weak impact on species diversity when geomorphological heterogeneity and area vary widely. Third, and most important, species richness peaked in refuges with intermediate levels of disturbance. This nonlinear relationship undermined the ability of multiple linear regression to identify a link between diversity and disturbance (Nichols 1996).

The fact that the combined effects of geomorphological heterogeneity and area accounted for less of the variance in species diversity in this study (multivariate $R^2 = 0.66$) than in the study by Harner and Harper (1976) (multivariate $R^2 > 0.98$) was likely a function of differences in habitat, disturbance regime, geomorphological factors measured, and sampling strategy. Harner and Harper (1976) focused on one community type (shrub dominated communities within the pinyon-juniper community type), selected locations based on uniformity of disturbance patterns, matched sampling sites at each location based on disparity of geomorphological heterogeneity, and calculated indices of geomorphological heterogeneity based on eight variables influencing water and nutrient availability to plants. The 26 ASRI refuges in this study supported 16 highly diverse community types with a wide range of disturbance patterns, adding substantially to the variability and complexity of the biota. In addition, only three geomorphological factors were measured, and refuges were not selected based on extreme expressions of geomorphological heterogeneity. The fact that geomorphological heterogeneity in these 26 diverse refuges was significantly related to plant species richness supports the conclusion that geomorpho-

logical heterogeneity is a consistent, robust predictor of biodiversity even when site size, community-type complexity, and disturbance vary widely.

Conclusions

Conservation efforts have recently focused on the preservation of biodiversity (Margulis et al. 1988) and entire ecosystems (Hunter et al. 1988; Scott et al. 1993) rather than on the protection of a single target species. As an addition to this genre of protection strategies, the conservation of geomorphological heterogeneity would enhance the long-term preservation of biodiversity because it is not subject to the vagaries of the transitory nature of contemporary plant communities. The paleoecological record clearly shows that most modern plant communities in North America are temporary assemblages, shifting in their abundance and distribution (Hunter et al. 1988). Significant climate changes predicted for the next century will likely heighten the ephemeral nature of plant communities (e.g., Kareiva et al. 1993). Because geomorphological heterogeneity and biodiversity have been demonstrated to be intricately linked in a suite of discontinuous landscapes that vary widely in size and disturbance regime, the conservation of geomorphological heterogeneity is likely to be an efficient strategy for conserving both extant and potential biodiversity.

Acknowledgments

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