

Effects of Spatial Heterogeneity of Microenvironment on Plant Biodiversity in the Southeastern Missouri Ozarks

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Abstract

In this paper we examine how the spatial heterogeneity of microclimate, topography, and vegetation influences plant species richness in the Southeastern Missouri Ozarks and how the results from this study related to the species richness-habitat heterogeneity hypothesis. We measured air temperature, soil temperature (5cm in depth), soil surface temperature, and soil moisture every 10 m along a 4250 m transect using mobile and permanent weather stations during the growing season, June to September 1996. We used 1 × 1 m plot to record ground flora (up to 2 m above ground) information, such as height and coverage, by species every 10 m along the transect. Topographic condition, litter depth, rock coverage, canopy coverage, and landscape patch type were also recorded at each plot. Elevation at each plot was measured using a submeter-resolution global positioning system (GPS). We find that the heterogeneity of topography, vegetation, and microclimate is strongly correlated with plant species richness ($R^2=0.99$), but the relationships are highly scale dependent. Most variables are highly correlated with plant species richness from 1500 to 2000 m scale. Contrary to the prediction of habitat heterogeneity theory, we find that the heterogeneity of slope and aspect is negatively correlated with plant species richness. The heterogeneity of elevation is weakly correlated with plant species richness. However, the heterogeneity of patch type, canopy coverage, and ground flora coverage is highly and positively correlated with plant species richness at most spatial scales examined. Plant species richness can be accurately predicted by the heterogeneity of microclimate. At 2000 m scale, spatial heterogeneity of microclimate can explain 98% of the total variation in plant species richness.

I. INTRODUCTION

Biodiversity is of worldwide concern among academic, public, and political communities because the current rate of loss of biological diversity is unprecedented in human history (Wilson and Peter 1988; Sharitz et al 1992). It is estimated that species are disappearing at a rate 1000-10,000 times faster than the historical rate of extinction and 20-50 percent of the world's total species will be lost over the next century (Pearce and Moran 1994). Human disturbances are commonly recognized as the major cause leading to the current loss of biodiversity (Wilson and Peter 1988; Finch 1992; Wickham et al. 1997). Scientists, resource managers, and policy makers are being challenged to preserve present species and restore the lost species in degraded ecosystems.

Ecologically, the loss of species results from the loss of their niches or habitats. Rowe (1992) points out that biodiversity depends on ecodiversity, which is defined explicitly as the diversity of the structures and patterns (e.g. topography and patch types) of landscapes and waterscapes in a specific area. Preserving and

enhancing habitat diversity are critical to conserving biodiversity, because increasing heterogeneity and complexity in the physical environment creates more complex and diverse plant and animal communities supported by that environment. (Pianka 1966; Probst and Crow 1991; Sharitz et al 1992; Bowman 1996). The habitat heterogeneity hypothesis, which was derived from observations that the more diverse islands had the higher species diversity (MacArthur and Wilson 1967), has been applied to explain many biodiversity hot-spots in the world. For example, the remarkably high species richness in Cape Peninsula, South Africa is due to the exceptionally high diversity of topography, climate, bedrock, soil, landscape structure, and vegetation history (Cowling et al. 1996; Simmons and Cowling 1996; Goldblatt 1997).

Numerous studies have shown that biodiversity from regional to continental scales is driven by climate as a proxy for available energy (Simpson 1964; Kiester 1971; Schall and Pianka 1978; Wright 1983; Currie 1991; Wickham et al. 1997). Brown (1981) reported

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that the maximum or potential species richness was constrained by energy at large scales, whereas species richness at small scales was primarily determined by available energy partitioning. Energy partitioning is also the driving mechanism in shaping microclimate at small scales. Therefore, microclimate may well reflect species richness at small scales.

The effects of topography and climate on biodiversity have been well documented (Zobel et al. 1976; Goldblatt 1997; Jones et al. 1997; Wickham et al. 1997; Bowman 1996; Birks 1996; Nevo et al. 1996; Chikatunov et al. 1997). Kerr and Packer (1997) find that the species richness-energy hypothesis applies to North American mammals only over a limited geographical area where climatic energy levels are low. In relatively high-energy regions of North America (i.e., lower latitude), they find that species richness is best predicted by topographic heterogeneity and local variation in energy availability rather than the mean available energy. Richerson and Lum (1980) find that topographic heterogeneity is positively and significantly correlated with plant species richness in California. However, Currie and Paquin's study (1987) shows that topographic heterogeneity (within quadrat variation) is not significant in explaining the variation in tree species richness in North America. Most previous studies were conducted at coarse scales (e.g. 2.5° × 2.5° latitude/longitude grid) and based on vegetation maps, faunal maps, topographic maps, climatic maps, or a limited number of weather stations (Richerson and Lum 1980; Currie 1991; Schall and Pianka 1978; Kerr and Packer 1997; Wright 1983; Currie and Paquin 1987). Few published studies have tested the species richness-energy hypothesis or the species richness-habitat heterogeneity hypothesis using direct field-collected data.

It is impractical to manage biodiversity at global, continental, or even regional level. Landscape or ecosystem management aimed at preserving biodiversity has been a widely accepted approach to natural resources management (Franklin 1993; Christensen et al. 1996; Ostfeld et al. 1997). Currie (1991) pointed out that the energy-richness relationship depends on scale, therefore, the conclusions drawn from continental or subcontinental level might not be applicable to the landscape level. However, few reported studies have examined the influence of such factors as climate, climate variability, habitat heterogeneity, history, available energy, competition, predation, and disturbance on species richness at landscape or smaller scales. Differences in the topographic relief (highest elevation minus lowest elevation) were commonly used in earlier studies as a heterogeneity indicator within sampling units to test the habitat heterogeneity hypothesis. The spatial heterogeneity of slope, aspect,

patch type, and vegetation coverage were generally neglected in earlier studies, but these factors may also influence species richness, especially in mountainous areas.

Our previous paper (Xu and Qi, 2000) examined how topography, microclimate, landscape patch type, and temporal variability of microclimate influence plant species richness in southeast Missouri Ozarks. In this paper we test: (1) how the spatial heterogeneity of topography and microclimate is correlated with plant species richness, and (2) how the relationships change with spatial scales.

II. METHODS

Study Area

The Missouri Ozark Forest Ecosystem Project (MOFEP), initiated by the Missouri Department of Conservation in 1990, is a pilot project to study the effects of different forest management practices on main ecological processes and functions. As a long-term ecosystem research project, MOFEP is composed of 10 subprojects that focus on: (1) composition and spatial distribution of woody vegetation, (2) herbaceous plant species diversity, (3) forest bird diversity and productivity, (4) oak *Quercus* spp. mast production, (5) density and diversity of small mammals, reptiles, and amphibians, (6) water movement and water quality, (7) forest litter invertebrates, (8) genetic diversity in selected woody plants, (9) nutrient cycling, and (10) landscape ecology and microclimate (Brookshire & Hauser 1993). Biodiversity study is a major part of this project.

The MOFEP is made up of 9 compartments, ranging in size from 260 to 527 ha, which are located in Carter, Reynolds, and Shannon counties in the southeastern Missouri Ozarks (91°01' to 91°13'W and 37°00' to 37°12'N). This area is 84% forested with large contiguous blocks separated only by roads and streams (Brookshire & Hauser 1993). Agricultural activities are limited to bottomland corridors along primary streams. The study area consists of mature upland oak-hickory and oak-pine forest communities. Dominant tree species include white oak (*Quercus alba* L.), black oak (*Quercus velutina* L.), post oak (*Quercus stellata* Wang.), scarlet oak (*Quercus coccinea* Muenchh.), blackjack oak (*Quercus marilandica* Muenchh.), chinkapin oak (*Quercus muehlenbergii* Engelm), shortleaf pine (*Pinus echinata* Mill.), maple (*Acer* spp.), and hickory (*Carya* spp.). Understory species include dogwood (*Cornus* spp.), sassafras (*Sassafras albidum*), and blackgum (*Nyssa sylvatica*).

Geologically, this region is underlain mainly by Ordovician age dolomite with areas of Cambrian age dolomite. Precambrian igneous rocks are also present (Missouri Geological Survey 1979). Weathering of the Ordovician and Cambrian age dolomites has resulted in a deep mantle of leached, very cherty residuum on the MOFEP study sites (Gott 1975). Soils on this area were formed mostly in residuum. The common series are Viburnum, Midco, Gepp, Bardley, Viraton, Poynor and Clarksville (Gott 1975). Mean annual temperature and annual precipitation are 13.3°C and 1120 mm, respectively.

Experimental Design and Instrumentation

Field experiments were conducted from June to September 1996. We used a 4250 m transect to sample microclimate and plant species. The transect was oriented in the south-north direction and its starting point was randomly located in MOFEP site 1. Since microclimate might have more influence on ground flora than on overstory, and because most important soil processes (e. g. horizontal rooting) occur between 5 and 20 cm from the soil surface (Faulkner 1976; Dickmann and Pregitzer 1992), we chose air temperature at 1.0 m above the soil surface and soil temperature at 5 cm in depth to represent the air temperature (T_a) and soil temperature (T_s) in this study. We also monitored soil surface temperature (T_{sf}) and soil moisture, for soil surface temperature may influence seedling mortality and soil moisture is critical for seed germination (Hungerford and Babbitt 1987; Kozlowski et al. 1991). Every 10 m along the transect we sampled T_a , T_s , and T_{sf} using mobile weather stations (custom-built thermocouple sensors). Each weather station covered 150 m along the transect. Continuous data collection at each station lasted for about two weeks. Type-T thermocouples were used to measure soil and soil surface temperature, and type-E thermocouples were used to measure air temperature. Campbell dataloggers (21X and CR10) were programmed to sample data every 10 seconds and to record 20 minute average values. TOSHIBA T1200 and T1000 portable computers and SC32A interfaces were used for programming and data retrieval.

Two permanent weather stations were installed in the experimental area, one in a forest opening and the other in a closed canopy forest. The purposes of the two permanent stations were: (a) to estimate any missing data resulting from technical failures in mobile stations; (b) to compensate for the limitation of sampling locations and times; and (c) to evaluate long-term microclimatic characteristics (seasonal, annual, or longer). Microclimatic variables monitored at the permanent stations included solar radiation, wind speed, wind direction, relative humidity, precipitation,

soil heat flux, soil moisture, soil temperature at depth of 0, 5, 10, 15, and 20 cm, and air temperature at 0, 0.5, 1.0, 1.5, and 2.0 m above the ground.

Vegetation plots (1 × 1 m) were sampled every 10 m along the transect to record species types and coverage of the ground flora (up to 2 m above soil surface) and to measure the height, diameter at breast height (DBH), distance to the plot center, and bearing of four trees closest to the plot. Canopy coverage was also measured at the center and each corner of the plot using a GRS densitometer (Forestry Suppliers, Inc.). We also estimated the coverage of litter, bare soil, rock, moss, and coarse woody debris (CWD) in each plot. A soil sample was taken in each plot to determine soil moisture. All the soil samples along the transect were taken on one day during typical weather conditions for each month (June through September). Soil samples were oven-dried for 24 hours at 105 °C to calculate soil water content (%). We located each sampling point (including elevation) along the transect using submeter-resolution global positioning system (GPS) (Trimble Navigation Limited) in November 1996, when most leaves fell off in order to improve GPS measurement accuracy.

Data Analysis

We used multiple regression techniques to fill the data gaps along the temporal scale. Air temperature (1 m above soil surface), soil temperature (5 cm in depth), and soil surface temperature at the two permanent stations were independent variables and the temperature along the transect was the dependent variable. Sample size was 1008 for most part of the transect and 504 for some plots due to instrumental failure. We used SAS (SAS Institute Inc.) to perform regression analysis and analysis of variance (ANOVA). All the regression equations used to fill the temperature data gaps were tested ($R^2 > 0.86$, $n > 504$).

There are a number of indices to quantify biodiversity. The commonly used Shannon-Wiener and Simpson's indices are not appropriate for this study because: (1) the large variation of species in each plot along the transect does not meet the assumption of the two indices that all species are represented in the sample; (2) Shannon index over-weights rare species and Simpson's index over-weights the most abundant species (Magurran 1988). We used species richness in this study as Whittaker (1972) and Pianka (1966) suggested that species number per unit area was the most generally appropriate measure of local or regional diversity because it weights rare and common species equally. Molina and Palma (1996) also found that Shannon-Wiener index was a poor indicator for butterfly diversity, and that richness is good measure-

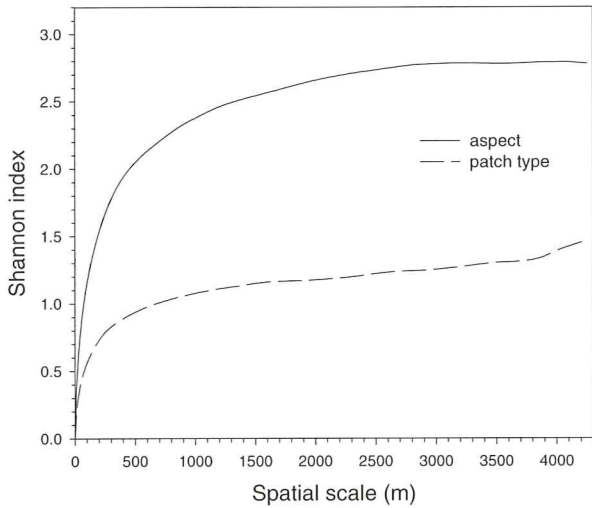


Figure 1. Spatial heterogeneity of aspect and patch type at different scales.

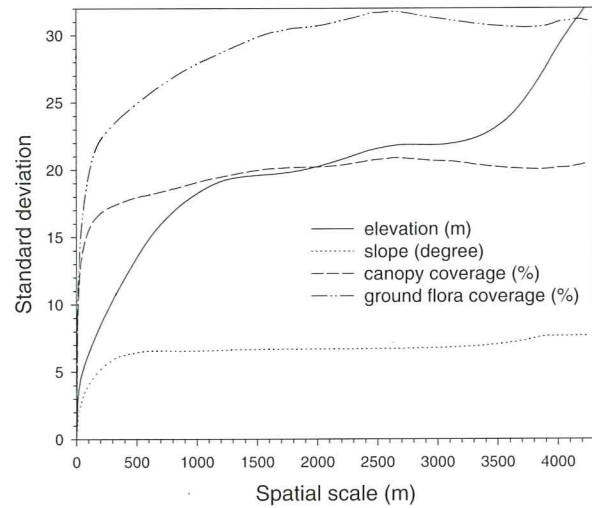


Figure 2. The effects of spatial scale on heterogeneity of elevation, slope, canopy coverage, and ground flora coverage.

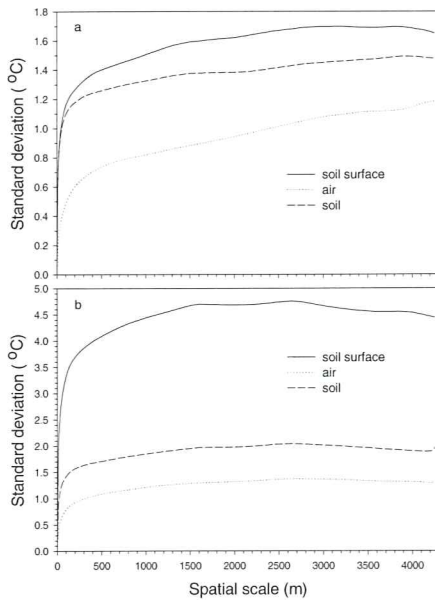


Figure 3. Spatial heterogeneity of temperature at different spatial scales: (a) seasonal minimum temperature, (b) seasonal maximum temperature

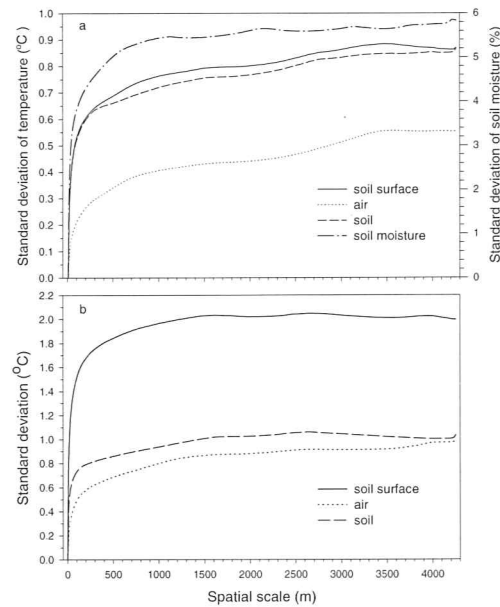


Figure 4. Spatial variation of seasonal mean temperature, soil moisture, and diurnal temperature range (DTR) at different spatial scales: (a) seasonal mean temperature and soil moisture, (b) DTR.

ment for site conservation assessment.

However, we used Shannon-Wiener index to describe the spatial heterogeneity of aspect and landscape patch type. Aspect was grouped every 20 degrees. We identified 12 major patch types in our study area. Standard deviation was used to evaluate the spatial heterogeneity of the other topographic and microclimatic variables. GPS data were differentially corrected according to base station data using Trimble's GPS Pathfinder software (Trimble Navigation Limited).

III. RESULTS

Spatial Heterogeneity of Topography, Canopy Coverage and Patch Type

Spatial heterogeneity of topography, canopy coverage, and patch type was highly scale dependent (Figure 1, 2). The influence of scale on the spatial heterogeneity of topography and vegetation was considerable, especially at small scales. The averaged Shannon-Wiener index for aspect changed from 0.31 at 10 m scale to

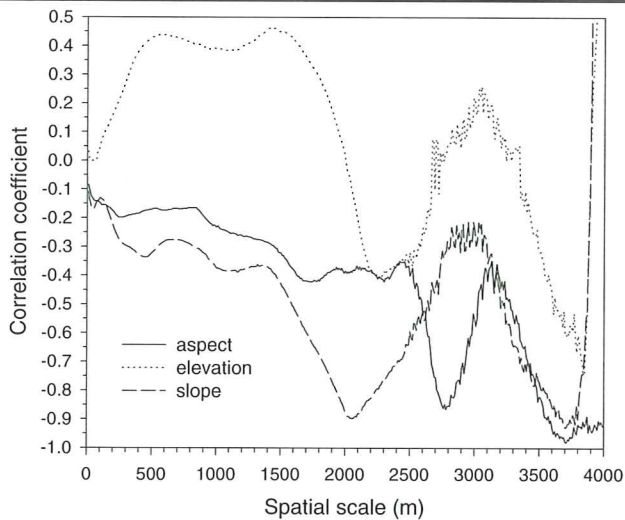


Figure 5. Correlation coefficients between plant species richness and the heterogeneity of aspect, slope, and elevation

2.7 at 4250 m scale. For patch type the index varied from 0.16 to 1.4 corresponding to the same range of spatial scale. Shannon-Wiener index for aspect increased rapidly from 0 to 1000 m scale and then it stabilized at about 2.5. For patch type the index increased quickly from 0 to 500 m scale, and stabilized around 1.0 (Figure 1).

The spatial variation of slope changed from 0 to 6 degrees as scale increased from 0 to 300 m, and then was quite stable at approximately 6 degrees as the spatial scale increased (Figure 2). The most rapid increase of spatial variation of canopy coverage and ground flora coverage occurred in the first 200 m scale. Ground flora had higher spatial variation than that of canopy coverage (Figure 2). The spatial variation of elevation increased rapidly from 0 to 1200 m scale, then was relatively stable before its second rapid increase from 3500 m scale (Figure 2).

Spatial Heterogeneity of Microclimate

The spatial variation of most microclimatic variables increased rapidly from 0 to 200 m scale. Beyond this scale the effects of scale on spatial variation became much weaker (Figure 3, 4). The influence of spatial scale on all the microclimatic variables had similar logarithmic pattern. Soil temperature (minimum, maximum, and mean) had a larger spatial variation than air temperature, but smaller than soil surface temperature. Seasonal minimum temperature (air, soil, and soil surface) had a smaller spatial variation than seasonal maximum temperature, but larger than seasonal mean temperature (Figure 3a, b, 4a). Diur-

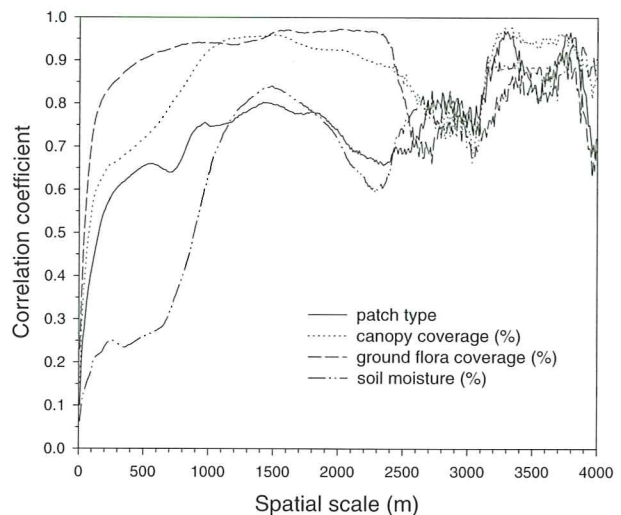


Figure 6. Correlation coefficients between plant species richness and the heterogeneity of patch type, canopy coverage, ground flora coverage, and soil moisture

nal temperature range (DTR) had a larger spatial variation than seasonal mean temperature (Figure 4b). Soil moisture had the same pattern of spatial variation as temperature and the standard deviation of soil moisture stabilized around 5.8% when scale was beyond 500 m (Figure 4a).

The Relationship between Plant Species Richness and Spatial Heterogeneity of Topography and Landscape Patterns

Plant species richness and the spatial heterogeneity of aspect and slope were negatively correlated and this correlation was highly scale dependent (Figure 5). At small scales they were loosely correlated, but their correlation coefficients reached -0.9 at about 2000 m scale for slope and -0.85 at 2800 m for aspect. The spatial variation of elevation, which is a major indicator of the spatial heterogeneity of landscape, was loosely correlated with plant species richness. Their correlation coefficient was positive when scale was smaller than 2000 m, then fluctuating between negative and positive as scale increases (Figure 5). The spatial heterogeneity of patch type, canopy coverage, ground flora coverage, and soil moisture was positively correlated with plant biodiversity at all scales (Figure 6). Plant biodiversity was highly correlated with the spatial heterogeneity of canopy and ground flora coverage when scale was larger than 200 m ($R > 0.8$). The influence of the spatial heterogeneity of patch type on plant species richness was significant when scale was larger than 1000 m ($R > 0.7$, $p < 0.05$). The high correlation between species richness and spatial heterogeneity of most topographic and

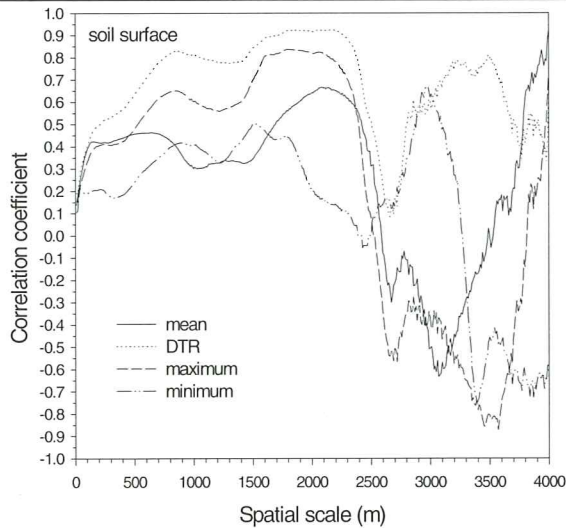


Figure 7. Correlation coefficients between plant species richness and the heterogeneity of seasonal mean, minimum, maximum, and diurnal temperature range (DTR) of soil surface temperature

vegetation variables occurred from 1500 to 2000 m scale (Figure 5, 6). At 2000 m scale, the spatial heterogeneity of topographic variables, mainly by slope, can explain 90% of the total variation in plant species richness ($p < 0.0001$) (Figure 5). From 200 to 2500 m scale, the spatial heterogeneity of vegetation coverage (overstory and ground flora) can explain about 95% of the total variation in plant species richness ($p < 0.0001$) (Figure 6). Of the 95% variation explained by vegetation coverage, the spatial heterogeneity of ground flora explains 94%, with the heterogeneity of canopy coverage and patch type contributing the remaining 1%.

The Relationship between Plant Biodiversity and Spatial Variation of Microclimate

The spatial heterogeneity of soil surface temperature (mean, minimum, maximum, and DTR) was positively correlated with plant biodiversity when scale was smaller than about 2500 m. Beyond 2500 m scale their relationships were more complicated (Figure 7). DTR and maximum temperature had larger correlation coefficients with species richness than minimum and mean soil surface temperature when scale was between 500 and 2500 m (Figure 7). The spatial variation of DTR and maximum soil surface temperature was significantly correlated with plant biodiversity at the same scale range ($0.75 < R < 0.91$, $p < 0.05$).

The spatial variation of mean and minimum air temperature was negatively correlated with plant biodiversity except under small spatial scales (< 500 m). Plant biodiversity was highly correlated with the spatial variation of mean air temperature when scale

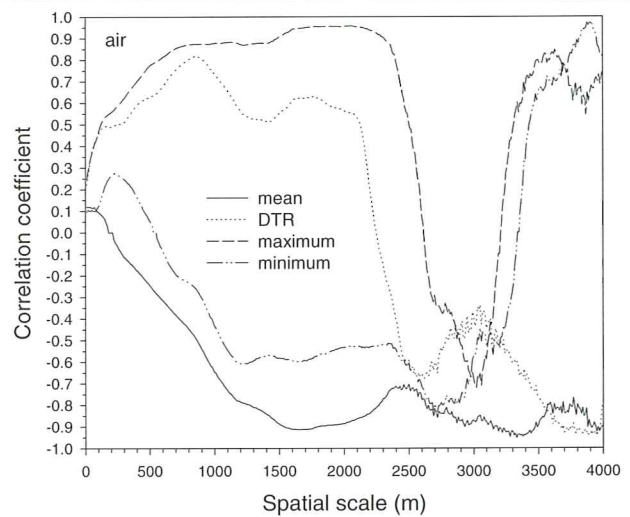


Figure 8. Correlation coefficients between plant species richness and the heterogeneity of seasonal mean, minimum, maximum, and diurnal temperature range (DTR) of air temperature

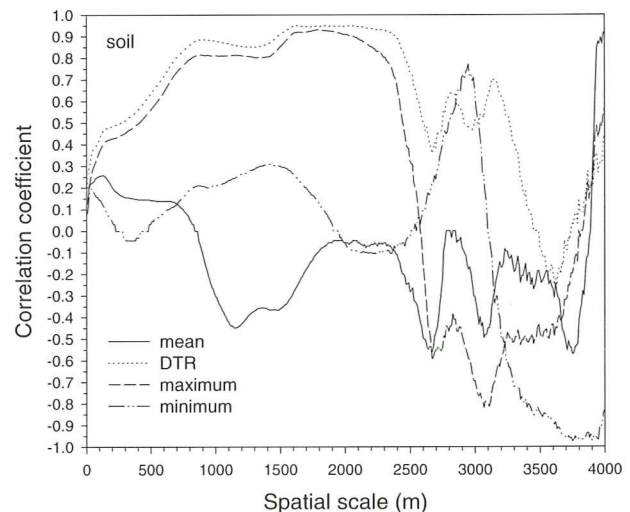


Figure 9. Correlation coefficients between plant species richness and the heterogeneity of seasonal mean, minimum, maximum, and diurnal temperature range (DTR) of soil temperature

was larger than 1000 m ($R < -0.8$) (Figure 8). The spatial variation of DTR and maximum air temperature was positively correlated with plant biodiversity when scale was smaller than 2200 m and the highest correlation coefficient reached 0.94 between 1500 and 2300 m scale (Figure 8). The highest correlation coefficient between plant biodiversity and spatial variation of seasonal minimum air temperature occurred at about 3800 m scale (Figure 8).

Plant biodiversity and the spatial variation of DTR and maximum soil temperature were positively correlated for scale up to 2500 m, and their correlation coefficients were greater than 0.8 when scale was be-

Table 1. Topography, vegetation, and microclimate variables used in this study and their regression coefficients in the final stepwise regression model (2000 m scale)

Environmental variable	Heterogeneity description	Coefficient
aspect	Shannon-Wiener index	
slope	standard deviation (degree)	-0.0318
elevation	standard deviation (m)	
patch type	Shannon-Wiener index	-0.1189
canopy coverage	standard deviation (%)	0.021
ground flora coverage	standard deviation (%)	0.0214
seasonal mean soil surface temperature	standard deviation ($^{\circ}\text{C}$)	-0.7536
DTR of soil surface temperature	standard deviation ($^{\circ}\text{C}$)	0.4527
seasonal maximum soil surface temperature	standard deviation ($^{\circ}\text{C}$)	-0.0862
seasonal minimum soil surface temperature	standard deviation ($^{\circ}\text{C}$)	-0.2615
seasonal mean air temperature	standard deviation ($^{\circ}\text{C}$)	
DTR of air temperature	standard deviation ($^{\circ}\text{C}$)	
seasonal maximum air temperature	standard deviation ($^{\circ}\text{C}$)	-0.1959
seasonal minimum air temperature	standard deviation ($^{\circ}\text{C}$)	0.1422
seasonal mean soil temperature	standard deviation ($^{\circ}\text{C}$)	0.4994
DTR of soil temperature	standard deviation ($^{\circ}\text{C}$)	-0.2046
seasonal maximum soil temperature	standard deviation ($^{\circ}\text{C}$)	
seasonal minimum soil temperature	standard deviation ($^{\circ}\text{C}$)	0.2233
soil moisture	standard deviation ($^{\circ}\text{C}$)	

Note: DTR - diurnal temperature range

tween 800 and 2400 m (Figure 9). However, the spatial variation of mean and minimum soil temperature was weakly correlated with plant biodiversity almost at any scale. The spatial variation of soil mean temperature was negatively correlated with plant biodiversity except at small scales (< 800 m) (Figure 9). Plant biodiversity and the spatial variation of soil moisture were positively correlated at any scale. Around 1500 m scale the spatial variation of soil moisture can explain about a half of the variation in plant biodiversity ($R > 0.7$) (Figure 6).

For most microclimatic variables, the spatial heterogeneity and plant species richness were highly correlated between 1500 and 2000 m scales (Figure 7, 8, 9). At 2000 m scale, the spatial heterogeneity of 13 microclimatic variables can explain 98% of the total variation in plant species richness. We used stepwise regression because of the colinearity between these microclimatic variables. The final model included 9 independent variables. The variables that were not included in the final model were the spatial standard deviations of seasonal mean, minimum, maximum soil temperature, and seasonal mean soil surface temperature.

In order to evaluate the total effects of spatial heterogeneity of topography, vegetation, and microclimate on plant species richness, we performed a stepwise regression using 19 environmental variables (Table

1). The total spatial heterogeneity can explain 99.3% of the total variation in plant species richness and the final regression model included 13 independent variables (Table 1).

IV. DISCUSSION

In this study, we used growing-season microclimatic and vegetation information to correlate with plant species richness. This can rigorously test the species-energy hypothesis since, as Turner et al. (1988) pointed out, the correlation should exist only during those parts of the year when organisms are actively absorbing energy, and should disappear if energy absorption ceases. Therefore, growing-season microclimatic variables are better than yearly climatic variables for this purpose.

This study shows that plant species richness at some spatial scales can be well predicted by the heterogeneity of topography, vegetation, and microclimate at the same scale. In addition, the influences of these variables on plant species richness depend on spatial scale. At 2000 m scale, the heterogeneity of microclimate is a better predictor of plant species richness than topography and vegetation.

Our results that the spatial heterogeneity of aspect and slope is negatively correlated with plant biodiversity and that the spatial variation of eleva-

tion is poorly correlated with plant biodiversity show that high topographic heterogeneity does not always produce high species diversity at the spatial scales examined. This result is inconsistent with the general species richness-habitat heterogeneity theory as supported by most previous studies (Pianka 1966; Sharitz et al 1992; Probst and Crow 1991; Bowman 1996; Currie 1991; Cowling et al. 1996; Simmons and Cowling 1996; Goldblatt 1997), but agrees to Currie and Paquin's (1987) conclusion that topographic heterogeneity is not significantly correlated with tree species richness in North America. We postulate that sharp topographic changes at small scale may limit species reproductive processes, such as seed distribution and pollination.

Another possible explanation on the negative correlation between heterogeneity of aspect and slope and plant species richness is that the heterogeneity of aspect and slope is positively correlated with elevation. Our previous study has shown that elevation is negatively and significantly correlated with plant species richness so that low elevation areas normally have high species richness in our study area (Xu and Qi, 2000). We have not found any previous studies incorporating the heterogeneity of slope and aspect in consideration of habitat heterogeneity. The result that topographic heterogeneity is weakly correlated with species richness also suggests that response of species richness to environmental heterogeneity (e.g. topographical variation) may not be continuous. It seems that small environmental variations do not affect plant species richness because their influence on energy allocation is not large enough to provide different niches for more species.

In this study we find that the spatial heterogeneity of canopy coverage, ground flora coverage, and landscape patch type is positively correlated with plant biodiversity at all scales. This suggests that vegetation coverage and patch type are more important for plant biodiversity of the ground flora at landscape or smaller scales. Therefore, forest management practice which can diversify landscape patches and vegetation coverage, such as selecting cut and small area clear-cut, may help to preserve plant biodiversity in our study area with large continuous tracts of forest. Microclimate is an integrative variable which reflects topography, vegetation, hydrology, and regional climate. Our previous studies have shown that relationship between microclimate and plant species richness is spatially scale dependent (Xu and Chen 1997, Xu and Qi, 2000). In this study we also find that the effects of spatial heterogeneity of microclimate on plant species richness are highly scale dependent. For the same microclimatic variable, its correlation with species richness is low at small scales but variably

high at larger scales. This relationship may also change with different microclimatic variables, e.g. seasonal maximum and mean air temperature. The fact that the spatial variation of soil moisture is positively correlated with plant biodiversity at all scales indicates that soil moisture is critical in preserve biodiversity in our study area. Indeed, recent study has shown that summer drought is one of the major factors threatening the regeneration of some species in this area (Jenkins and Pallardy 1995).

Our study also shows that scale is critical in understanding and preserving biodiversity. The effects of environmental variables on biodiversity are highly scale dependent. We suggest that scale effects be taken into account in any landscape management activities aiming at preserving or enhancing biodiversity (Qi and Wu 1996).

V. CONCLUSION

The relationship between species richness and the heterogeneity of topography, vegetation, and microclimate is highly scale dependent. Most of these variables are highly correlated with plant species richness from 1500 to 2000 m scale. Contrary to the prediction of habitat heterogeneity theory, we find that the heterogeneity of slope and aspect is negatively correlated with plant species richness. The heterogeneity of elevation is weakly correlated with plant species richness. However, the heterogeneity of patch type, canopy coverage, and ground flora coverage is highly and positively correlated with plant species richness at most spatial scales examined. Plant species richness can be accurately predicted by the heterogeneity of microclimate. At 2000 m scale, spatial heterogeneity of microclimate can explain 98% of the total variation in plant species richness.

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