Ecology, 86(11), 2005, pp. 3039–3047
© 2005 by the Ecological Society of America

ELEVATIONAL SPECIES RICHNESS PATTERNS EMERGE FROM MULTIPLE LOCAL MECHANISMS IN HIMALAYAN WOODY PLANTS

Meera Anna Oommen[1,2] and Kartik Shanker[2,3]

[1]*Wildlife Institute of India, P.O. Box 18, Chandrabani, Dehradun 248001 India*
[2]*Ashoka Trust for Research in Ecology and the Environment (ATREE), 659, 5th A Main Road, Hebbal, Bangalore 560024 India*

Abstract. We compared woody plant species distributions across nested spatial scales (local scale to entire Western Himalaya) and explored landscape scale patterns in detail to obtain inferences about the elevational gradient in species richness. Distribution data were compiled for 1100 species in the Western Himalaya, and primary data, comprising 123 species and 47 000 individuals, were collected for a landscape. Correlates of diversity were examined for the five spatial scales, and for different biogeographic groups at the landscape scale. The results indicate multiple mechanisms both within and across scales. At the landscape scale, though the mechanisms explaining unimodal species richness patterns were hard to separate, the underlying correlates of biogeographic groups were more distinct; temperate species richness followed mid-domain model predictions, and showed a nonlinear relationship with temperature, whereas tropical species richness tracked temperature and area. Simulations demonstrated that models with varying assumptions, while resulting in monotonic, unimodal, or multimodal patterns at local scales, could all lead to unimodal patterns at regional scales when multiple local replicates are aggregated, with a peak in the major ecotone. The turnover or successive accumulation of marginal species in ecotones potentially explains the mid-elevational peak in this zone. Landscape scale primary data on distribution and abundance could therefore be critical to understanding key aspects of macroecological patterns.

Key words: elevational gradients; Himalaya; macroecology; mid-domain effect; plants; spatial scale; species richness.

INTRODUCTION

Macroecological studies of elevational species richness gradients have demonstrated monotonic, unimodal, and multimodal patterns (Whittaker 1960, Shmida and Wilson 1985, Stevens 1992, Rahbek 1997, Patterson et al. 1998, Grytnes and Vetaas 2002), of which unimodal patterns are reported to be most common, at least at large spatial scales (Rahbek 1995, 2005, Colwell and Lees 2000, Grytnes and Vetaas 2002, McCain 2005). The mechanisms underlying these patterns have been derived from and examined largely in the context of those proposed to bring about the latitudinal gradient in species richness (Stevens 1992). Conventional explanations for species richness patterns include the influence of factors such as area, temperature, energy and productivity, topographical and historical factors (Rosenzweig 1995, Rahbek 1995, 1997, Lomolino 2001, Brown et al. 2004). Additionally, the exploration of null models demonstrating ‘‘non-biological’’ patterns (Colwell and Hurtt 1994, Lyons and Willig 1997) led to the prediction of the mid-domain effect (MDE), which predicts that geometric constraints imposed by hard boundaries result in greater overlap of species ranges in the middle of sample domains, leading to an emergent mid-domain peak in richness (Colwell and Lees 2000).

Most of the proposed mechanisms are aimed at explaining the broad large-scale unimodal patterns and do not give a clear indication as to why monotonic and multimodal patterns are also occasionally observed along smaller spatial scales such as local slopes and landscapes. The nature of large-scale richness patterns may change with spatial grain and scale (Rahbek 2005), and there is clearly a need to explore the interconnectedness of large- and small-scale patterns (Storch and Gaston 2004, Storch et al. 2005). The dearth of such analyses is partly due to constraints such as the nature of data sets and methodology in macroecology (especially dependence on secondary distribution data), and the multiplicity of proposed mechanisms. Empirical as well as theoretical explorations of patterns across nested scales and representative geographical regions would add significantly to our understanding of macroecological gradients (Storch et al. 2005).

Most data sets that are used to address macroecological questions comprise species that can be grouped on the basis of their ecological and biogeographic affinities. On the basis of these characteristics, species occurring in a region can be classified within different biogeographic groups, guilds, or other meaningful eco-

Manuscript received 5 December 2004; revised 12 April 2005; accepted 13 April 2005. Corresponding Editor: T. J. Stohlgren.

[3] Corresponding author: E-mail: kartik@atree.org

logical groups. Extensive elevational gradients often encompass a number of distinct biomes, primarily the tropical and temperate communities. Many taxa including plants can be categorized into well-defined groups of species belonging to tropical, temperate, or cosmopolitan families. Tropical–temperate comparisons have been examined in many contexts (e.g., Coley and Barone 1996, for herbivory), and have recently been explored in macroecological studies of taxa such as small mammals (e.g., McCain 2005). The ecological or biogeographical attributes of species reflect, in essence, the sum total of their responses to various climatic, biological, and historical factors. Thus, it can be argued that different mechanisms will affect the richness of different groups.

Some explanations for the difference in diversity between tropical and temperate regions are based on differences in range sizes and other properties of species belonging to these groups. A plausible mechanism that emphasizes such differences between groups of species is the Rapoport effect (Stevens 1992), which proposes that high species diversity in lower latitudes (or altitudes) is generated by temperate (or higher altitude) species with high tolerance to climatic variability (and therefore more extensive ranges) intruding into marginal habitats (‘‘rescue effect’’ of Brown and Kodric-Brown [1977]). Additionally, it has also been proposed that the ecotones or the zones of interdigitation between communities support high species richness (Lomolino 2001, McCain 2005). If we look at this pattern within the framework of such a rescue effect and the ecotone as a marginal habitat for both tropical and temperate species (as opposed to just the lower elevations as predicted by Stevens), the overlap between the groups would significantly affect richness in the middle elevations, which in turn could affect patterns within and across scales.

In this study, we explore multiscale patterns of species richness in the Indian Western Himalaya. The Himalaya is an extensive yet unstudied biogeographic region with only a single macroecological study on large-scale plant diversity in the Nepal Himalaya (Grytnes and Vetaas 2002). We address three questions. (1) What is the pattern across scales in woody plant richness along an elevational gradient in the Indian Western Himalaya? (2) What are the correlates of species richness at a local (landscape) scale and are there differences between biogeographic groups of species? (3) What synthetic theory could explain patterns both within and across scales? First, we examine species richness patterns and their correlates across five nested spatial scales ranging from a single mountain slope to the entire Western Himalaya. At an intermediate landscape scale, we examine the effect of environmental factors, abundance, available area, and the mid-domain effect on tropical, temperate, and cosmopolitan groups of species. Finally, we use a simulation model incorporating multiple mechanisms and an ecotone effect to explore how multiple local-scale patterns might produce a unimodal regional pattern.

METHODS

Study area and data sets

The biogeographic affinities of the Himalayan region are a complex mixture of Palaearctic, Indo-Malayan, and Mediterranean elements and the Himalaya is considered to be the meeting place of these three realms. The three large nested geopolitical units in this study were the Indian Western Himalaya (~30° N–34°10′ N and 73°45′–80°40′ E; ~200 000 km^2), Uttaranchal State (~49 000 km^2), and the former Chamoli District (~7000 km^2; before 1999 this included the present Rudraprayag District). The two small spatial scales included a landscape scale field study site (~300 km^2) in Kedarnath Musk Deer Sanctuary (30°25′–30°45′ N, 78°55′–79°22′ E), and Bantoli, a single mountain slope of ~30 km^2, within it (five nested spatial scales and primary and secondary data collection sites are shown in Fig. 1, and data sources are shown in Appendix A).

Primary data collection was carried out in the Kedarnath Sanctuary along a topographically distinct temperate forest gradient (1500–3500 m) with a large number of tropical elements, both in terms of the number of species as well as their abundances. Temperate forests begin at 1500 m, above which the topography of the Himalaya changes significantly and altitudinal gain occurs over small spatial scales. The upper limit at 3500 m is the tree line, which is a limit for woody perennials. Anthropogenic influences on forests in the sampled gradient are minimal as permanent settlements are only situated below the lower elevational limit and most of the region is inaccessible, especially in winter.

For the three large spatial scales (Western Himalaya, Uttaranchal State, Chamoli District), we compiled woody plant distribution and altitudinal data from secondary sources (Appendix A). Secondary data from regional floras and checklists were used to determine the altitudinal distribution and geographical extent within the Himalaya for >1100 species. Altitudinal ranges were interpolated from the altitudinal limits of occurrence. For the two small spatial scales (Kedarnath Sanctuary and Bantoli mountain slope), primary data were gathered by stratified random sampling of all broad vegetation types in the intensive study area. These included lower and middle temperate oak (1500–2500 m), subalpine higher oak–fir forests (2500–3000 m), and the tree line (3100–3500 m). A total of 547 10-m-radius plots were sampled once and ~47 000 individuals belonging to 123 species were enumerated. For all woody stems, dbh (diameter at breast height) was measured and height was visually estimated. Sampling was roughly in proportion to available area of the main forest types. Maximum available areas were in the middle elevational zones; sampling area was limited in the lower elevations; species accumulation

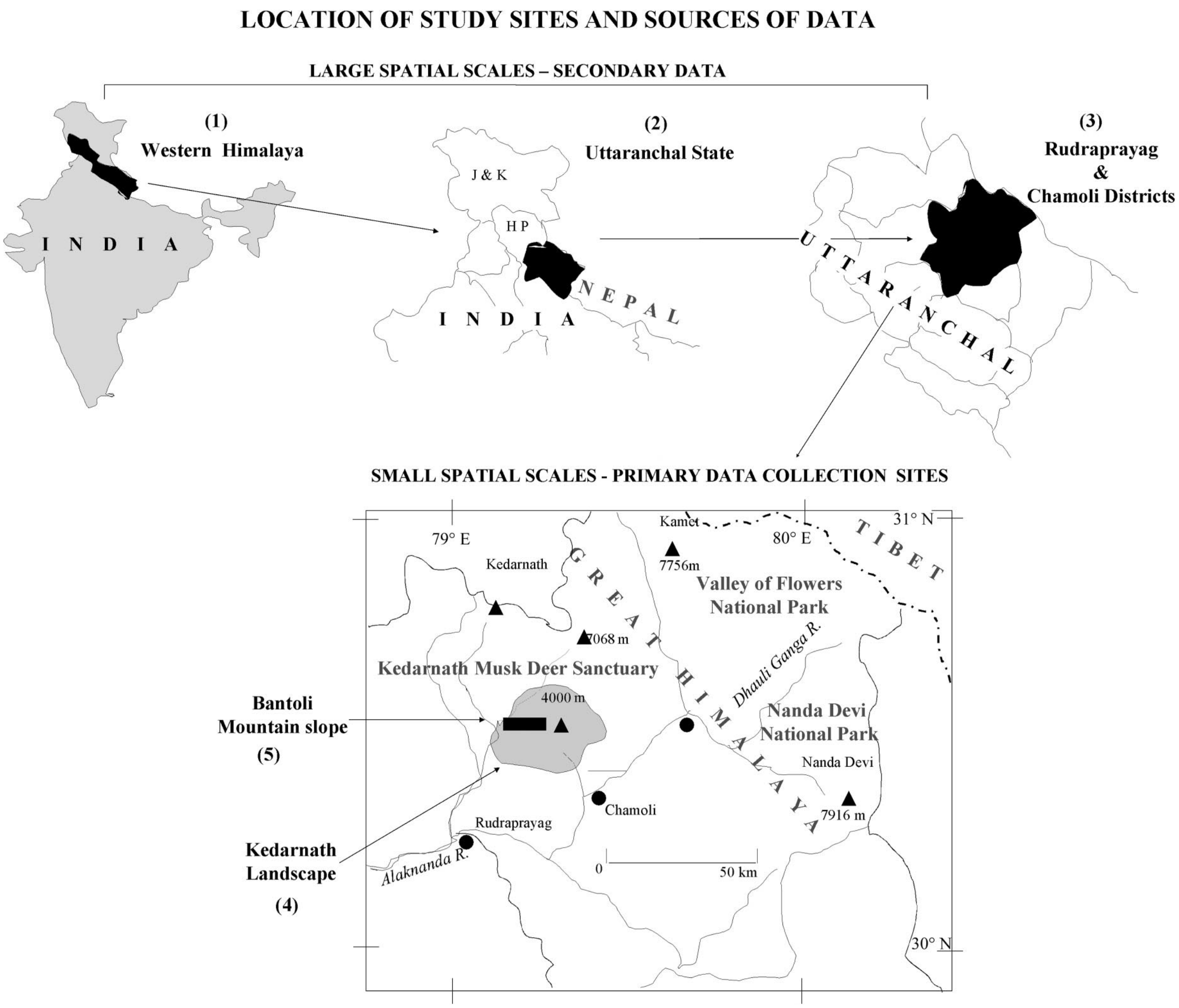

FIG. 1. The study area: the five nested spatial scales (labeled 1–5) and the type of data collected from each scale are shown. Complete descriptions of the sources for the secondary data are given in Appendix A.

curves for forest types reached an asymptote indicating that sampling was adequate. Soil samples (300 gm of soil up to a depth of 20–30 cm) were collected from all 547 plots, out of which 100 were randomly chosen for analysis. Six soil variables (pH, organic carbon, nitrogen, phosphorus, potassium, and water holding capacity) were quantified.

Analysis of correlates of species richness

Species richness (band sum) was compiled for 200-m elevational bands. Five correlates of species richness were examined (see Table 1). These included the effect of area (calculated for each elevation band from reliable digital elevation models derived from high resolution topographical maps, at scales 1:25 000 and 1:50 000), congruence with the null distributions predicted by the mid-domain effect (Colwell and Lees 2000), and environmental factors (rainfall and temperature). Other correlates included abundance, density, and biomass (basal area × height) at the landscape scale. Published summaries of net primary productivity were not available for the two largest scales; a rough surrogate for the intermediate scale (Chamoli District) could be gathered from only two secondary sources (Singh and Singh 1992, Singh et al. 1994). For the mid-domain effect, all models were explored, but detailed analysis was carried out for a one-dimensional model that selects ranges at random from the empirical range size distributions and places them randomly in the domain (Model 4 of RangeModel, see Colwell 2000). For comparisons with the mid-domain models, we used only species with their range limits within the domain as suggested by its proponents (Colwell et al. 2004).

At the landscape level, species were further subdivided into groups with cosmopolitan, tropical, and temperate affinities. This classification was based on existing information on species affinities derived from the literature. We divided the gradient (2000 m) into 100-m classes; smaller class widths would not have been ecologically meaningful due to spatial autocor-

TABLE 1. Correlates of species richness at different spatial scales.

Scale	Region	Altitude range (m)	Type of data	Area		Mean annual temperature		MDE† Model 4	
				r	*P*	*r*	*P*	*r*	*P*
Entire range	Western Himalaya	0–5000	secondary	*0.62*	*0.001*	*0.82*	*0.0001*	0.45	0.02
	subset	1500–3500	secondary	*0.88*	*0.0003*	*0.96*	*0.0001*	0.2	0.53
Regional	Uttaranchal State	0–5000	secondary	*0.54*	*0.008*	*0.90*	*0.0001*	0.3	0.12
	subset	1500–3500	secondary	*0.85*	*0.0007*	*0.96*	*0.0001*	0.17	0.57
Regional	Chamoli District	1500–3500	secondary	*0.74*	*0.014*	0.49	0.14	*0.91*	*0.0002*
Landscape	Kedarnath	1500–3500	primary	*0.79*	*0.01*	0.24	0.50	*0.75*	*0.01*
Single slope	Bantoli	2000–3500	primary	NA		*0.77*	*0.008*	0.3	0.34

Notes: Pearsons's correlations (r) for species richness at different spatial scales with predictor variables; $n = 25$ altitudinal classes where the altitudinal range extends from 0 to 5000 m, and $n = 10$ in all other cases. Values set in italics denote correlations significant at $P < 0.05$ with a Bonferroni correction. Bonferroni corrections were applied by dividing α by 3, the number of comparisons for each dependent variable, and checking significance at $P < 0.017$.

† Mid-domain effect.

relation. This resulted in 20 classes (i.e., $n = 20$ for most comparisons); all models were evaluated using univariate regressions. Spatial autocorrelation was checked using the spatial module of S-PLUS 4.5 (S-PLUS 2000); significance of Moran's coefficients were examined for a lag of 1 (i.e., neighbors consisting of only adjacent elevations; Appendix B). All significant correlations were tested by resampling the data to overcome the influence of individual data points and spatial autocorrelation (i.e., each model was reevaluated using a sample of 10 random data points, out of 20, and recalculating the regression parameters); 1000 resamples were calculated for each pair. Correlations were considered as significant only if >95% of Bonferroni-corrected resample coefficients were significant. We also analyzed the data at 200-m intervals, where there was no spatial autocorrelation in richness or in the residuals of regression models; results were identical to results from 100-m class analyses (Appendix C). All statistical analyses were carried out in S-PLUS.

Simulation model

We used a simulation model to explore the effect of scale on species richness patterns (details, including an analytical solution, are provided in Appendix D). We explored three scenarios (temperature dependence, the mid-domain effect, and a combination of the two) to simulate species distributions for a single replicate or mountain slope, comparable to local-scale data. For each of the simulations, the temperature dependence model assumed a linear relationship between tropical (positive) and temperate (negative) species and temperature, while the mid-domain effect model distributed species within each biome based on random range sizes and midpoints (Colwell and Lees 2000). Species distributions were modeled separately for tropical and temperate species and combined to generate species richness for each replicate; the gradient was divided into 20 classes, and tropical species were assigned to classes 1–15 and temperate species to classes 6–20, with an overlap of 10 classes. We also modeled another scenario for limited overlap between groups where the number of overlapping classes was only two. Using the above models, species distributions were first generated for 50 tropical and 50 temperate species for a single replicate. This process was repeated for 100 replicates. Regional species richness at each altitude (as is usually obtained from secondary data) was then derived by aggregating species distributions across several individual replicates; 2, 3, 5, and 10 replicates were aggregated to obtain regional species richness at different scales. Each aggregation was averaged from 100 combinations of replicates. Model simulations were written in S language and carried out in S-PLUS 4.5 (S-PLUS 2000).

RESULTS

Species richness patterns

At the three larger spatial scales in the Western Himalaya, Uttaranchal State, and Chamoli District, the number of species listed were 1100 (489 genera, 134 families), 926 (449 genera, 122 families), and 261 (104 genera, 51 families), respectively. At the landscape scale, 47 000 individuals of 123 species (70 genera and 40 families) were recorded in 547 plots, while Bantoli mountain slope recorded 61 species (42 genera, 30 families). Species richness patterns were unimodal (Fig. 2a), with a large number of range limits in the tropical temperate ecotone (Fig. 2b). At the landscape scale, species richness showed a hump-shaped realtionship with elevation; species with tropical, temperate, and cosmopolitan affinities accounted for 24%, 48%, and 28% of overall species richness. Expectedly, species belonging to tropical, temperate, and cosmopolitan families showed different patterns of distribution with peaks in different elevational zones (Fig. 2c).

Correlates of species richness

Species richness at larger spatial scales was analyzed with available data (temperature, area, and mid-domain models; Table 1). At the two largest scales, species richness was strongly correlated with temperature, both

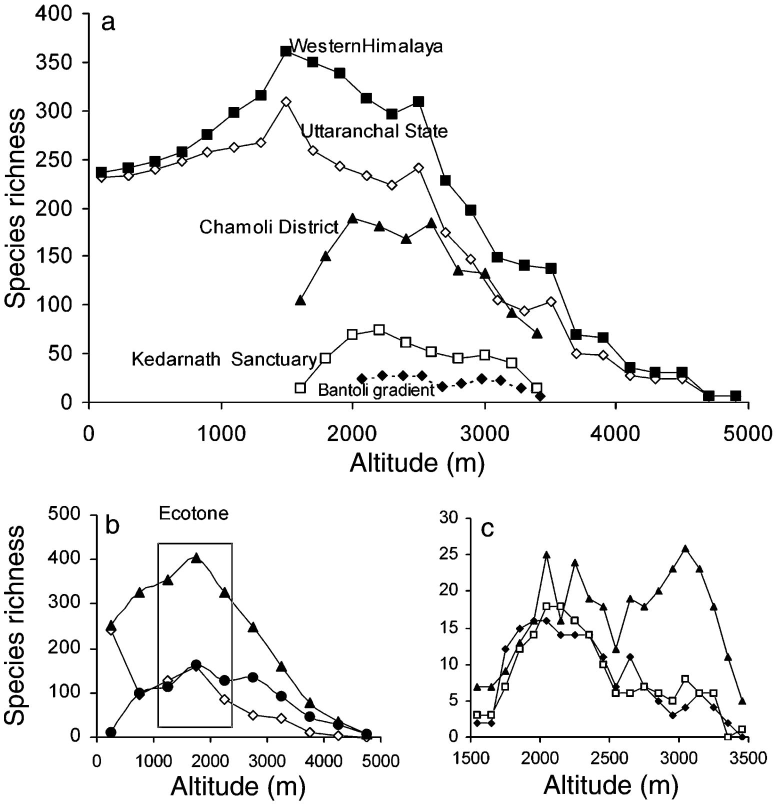

FIG. 2. Patterns of species richness: (a) species richness at five nested spatial scales, from a single slope to the entire Western Himalaya; (b) species richness in the entire Western Himalaya (solid triangles), with the number of species with upper limits (solid circles) and lower limits (open rhomboids) of ranges in each altitudinal class (the large rectangle shows the major ecotone in the Himalaya, and this represents the region of overlap between temperate and tropical communities); (c) at the landscape scale, species richness of different biogeographic groups including tropical (solid rhomboids), temperate (solid triangles), and cosmopolitan species (open squares).

for the complete gradient and for a subset in the middle elevation from 1500 to 3500 m. Richness was correlated with area in Chamoli District, where the gradient extended from 1500 to 3500 m and at the larger spatial scales. The correlations with area were even stronger at these larger scales, when a subset of elevations from 1500 to 3500 m was considered. There was a significant correlation with the predictions of the mid-domain model in Chamoli District, but not in Uttaranchal State or Western Himalaya, either for the entire gradient or for the subset of elevations from 1500 to 3500 m. At the landscape scale, overall species richness was significantly correlated with the predictions of the mid-domain model; there was a weaker relationship with area and abundance (Table 2).

For the groups, temperate richness was strongly correlated only with the mid-domain model. Temperate richness showed a bimodal relationship with temperature. For temperate richness, we expected a unimodal relationship with temperature; the presence of subalpine meadows with low richness in between could have caused this pattern. Cosmopolitan species richness was correlated with the predictions of the mid-domain model and, to a lesser extent, with the number of individuals in each altitude class. Tropical species richness was correlated with the density of individuals and to a lesser extent with area (Table 2, Fig. 3). When significant regression models were reevaluated with a Bonferroni correction applied (Table 2), overall richness, as well as the richness of the temperate and cosmopolitan groups, was significantly correlated only with the mid-domain model. Tropical richness on the other hand showed a very strong relationship with temperature, particularly when lower edge classes were treated as outliers and excluded. For these 18 classes, Bonferroni-corrected correlations of temperature with overall species richness, cosmopolitan species richness, and temperate species richness were not significant. For comparison, all other correlations were repeated for these classes, but did not change significantly.

None of the six soil variables was significantly correlated with species richness; principal components analysis Factor 1 (92%) and Factor 2 (7.5%) were not significantly correlated with species richness variables, number of individuals, or basal area. Tree biomass (which was correlated to net primary productivity at the regional scale) was used as a correlate of productivity. Mean biomass per plot was correlated with land-

TABLE 2. Correlates of species richness for different biogeographic groups.

Species richness	Abundance	Density	Area	Mean annual temperature	Soil PCA1	Biomass	MDE model
Overall richness	0.67** (850, 0)	0.39	*0.72**** (*969*, *209*)	0.26	0.03	0.60**,^{18} (454, 0)	*0.82**** (*1000*, *999*)
Cosmopolitan species	*0.82**** (*1000*, *923*)	0.11	*0.74**** (*1000*, *478*)	0.43	0.00	0.28	*0.90**** (*1000*, *1000*)
Temperate species	0.01	−0.40	0.33	−0.27	0.18	0.08	*0.94**** (*1000*, *1000*)
Tropical species	0.58** (255, 0)	*0.82**** (*1000*, *923*)	*0.80**** (*1000*, *799*)	0.52* (282, 0)	−0.17	*0.77***,^{13} (*1000*, *752*)	*0.73*** (*960*, *203*)

Notes: Pearsons's correlations (r) for overall species richness and for cosmopolitan, temperate, and tropical groups with predictor variables; $n = 20$ altitudinal classes, unless otherwise indicated by a superscript number. Bonferroni corrections were applied by dividing α by 7, the number of comparisons for each dependent variable, and checking significance at $P < 0.007$. Values in parentheses are the numbers of significant bootstrap correlations and Bonferroni-corrected bootstrap correlations. Values set in italics denote bootstrap correlations significant at $P < 0.05$.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

scape species richness, but residuals were not normally distributed (Table 2). Mean biomass per plot was correlated with tropical species richness at the landscape scale (Table 1).

Simulation model results

Four exploratory models are presented (Fig. 4). Tropical and temperate species (50 of each) were assigned to domains with a total of 20 classes (as in observed data) that overlapped in the central region. The temperature-dependent model showed maximum species richness at the lowest and highest elevations, but as species accumulated in the overlap zones, a unimodal pattern was predicted after just three replicates (mountain slopes) were combined to generate a regional pattern (Fig. 4a). When both tropical and temperate species were assigned a mid-domain model, the resulting pattern for a single slope was a unimodal pattern when there was extensive overlap (of 10 classes) between tropical and temperate species (Fig. 4b), and a bimodal pattern when there was low overlap (two classes; Fig. 4d). However, both show unimodal patterns once data from several slopes are aggregated. Based on observed patterns, we also modeled a combination of parameters, where tropical species tracked temperature and temperate species followed a mid-domain pattern (Fig. 4c). The simulated outputs also resulted in a unimodal pattern that resembled observed data for the largest spatial scales.

DISCUSSION

Species richness patterns across scales and groups

In this study, woody plant diversity at large spatial scales showed a unimodal relationship with altitude, with the peak in richness in the middle elevations. This pattern is typical of many mountain systems, and the only other published macroecological study from the

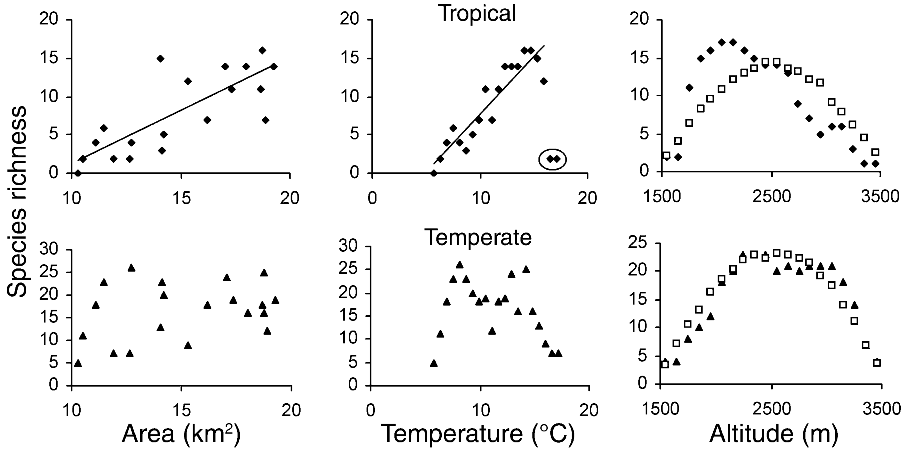

FIG. 3. Correlates of species richness. In the top three panels, tropical species richness (solid rhomboids) is correlated with area ($y = 1.4x - 12.6$, $r^2 = 0.64$, $n = 20$, $P < 0.001$) and with mean annual temperature when the lowest two altitude classes are excluded ($y = 1.5x - 7.6$, $r^2 = 0.85$, $n = 18$, $P < 0.0001$). In the lower three panels, temperate species richness (solid triangles) is not correlated with area or with mean annual temperature, but it is correlated with the predictions of the mid-domain model (see Table 2). For the mid-domain model, observed species richness (solid symbols) and predicted richness (open squares) are plotted against altitude to assess visual fit.

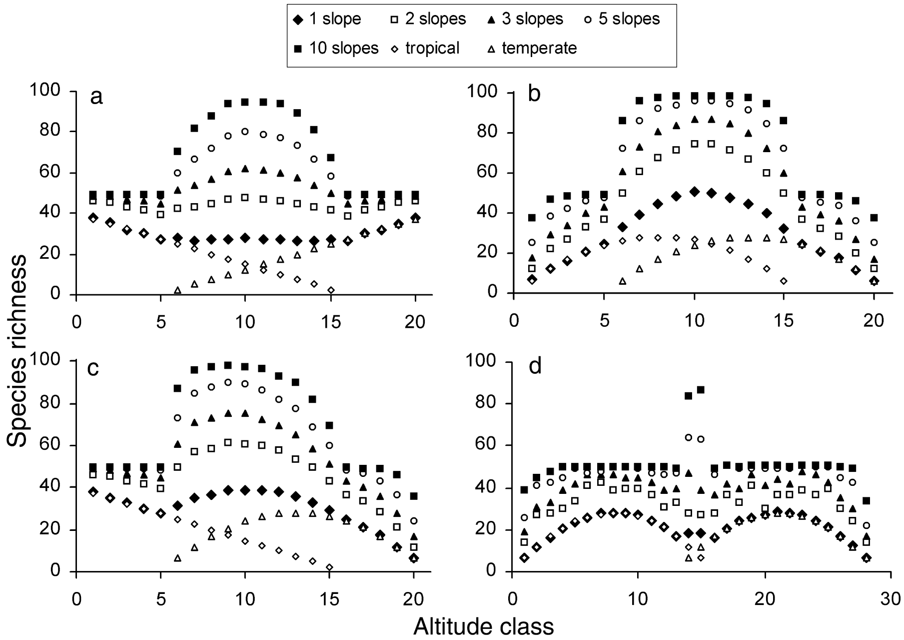

FIG. 4. Simulating species richness at different spatial scales: species richness patterns were simulated separately for tropical species (open rhomboids) and temperate species (open triangles) and combined to derive patterns for a single slope or local scale (solid rhomboids). Regional species richness patterns were derived by combining the data for two slopes (open squares), three slopes (solid triangles), five slopes (open circles), and 10 slopes (solid squares). Simulations were carried out for models where (a) both tropical and temperate species tracked temperature, (b) both groups followed predictions of the mid-domain model, (c) tropical species tracked temperature, and temperate species followed the mid-domain model, and (d) both groups followed predictions of the mid-domain model but had very little overlap. The *y*-axis represents predicted values of species richness in each of the altitudinal classes.

region in the adjoining Nepal Himalaya also reports a unimodal pattern (Grytnes and Vetaas 2002). In many regions, at smaller spatial scales such as landscapes and local gradients, there is evidence of typical unimodal patterns (as shown by data presented in this study), as well as occasional monotonic (Grytnes 2003, for Norwegian plants) and multimodal patterns in plants and other taxa such as birds (R. Raza, *personal communication,* for the Western Himalaya) and small mammals (McCain 2005, global study). Although data were available only for a limited number of factors for the larger spatial scales, available evidence points to different correlates at different scales. At the two largest scales (i.e., the Western Himalaya and Uttaranchal State), temperature showed the best fit, followed by available area. The influence of mid-domain effect seems limited at these scales and could be overshadowed by area, temperature, and energy-related factors. At intermediate scales (Chamoli District and Kedarnath Sanctuary), the mid-domain model showed the best fit. In this study, overall landscape species richness was correlated with a number of factors but the primary correlation was with the mid-domain effect.

For the biogeographic groups, the patterns were far clearer with temperate and tropical species showing different trends. Temperate species richness approximated the predictions of the mid-domain model and showed a nonlinear relationship with temperature. These species have been predicted to have larger environmental tolerances (Stevens 1992) and they may follow a random distribution within a broad bioclimatic zone (the limits of the temperate domain) defined by temperature and other environmental factors. Species with tropical and cosmopolitan affinities on the other hand seem to track a number of factors, primarily area and temperature. Tropical species are believed to have narrower tolerances to environmental variation and are likely to be affected by the steep temperature gradient and the amount of area available within this particular environmental window.

An ecotone accumulation effect on regional richness

An ecotone effect (high diversity in the ecotone due to significant overlap between communities) has been proposed in the context of elevational gradients and source–sink dynamics (Lomolino 2001) but has received very little attention. We focus on a significant aspect of this concept by exploring the ecotone effect in the context of multiple spatial scales. We propose that the position of the diversity peak is likely to be scale dependent, i.e., at the very local scales, species diversity will be higher in the middle of the major biological communities (e.g., subtropical/temperate/tropical) but is likely to shift to the ecotone as more mountain slopes (and marginal species) are added to the data set. The proportion of species shared and the amount of overlap between communities across spatial scales can play a significant role in determining this shift. Although the underlying mechanisms may be different for groups of species, simple model simulations show that these could still lead to unimodal species richness patterns at local and larger spatial scales. In our analyses, though two out of the four simulation models show bimodal or monotonic patterns at the smallest spatial scale, a unimodal pattern is inevitably formed after a small number of local slopes or replicates are pooled.

This can be explored further by looking at the contribution of marginal/sink species to the richness dynamics in the zones of overlap. Along a local gradient, in contrast to within biome richness that peaks in the middle, richness in the ecotone is likely to be composed of ecotone specialists and a number of low abundance sink species contributed by spillover from adjoining biomes (vis a vis the rescue effect hypothesis of Brown and Kodric-Brown [1977], mass effects of Shmida and Wilson [1985]). At a local gradient, the ecotonal richness may not be larger than the richness within biomes. However, when several local gradients are pooled to make a larger regional gradient, a larger number of sink species are likely to accumulate and inflate species richness of the ecotone (in comparison to the middle of a domain). Essentially, each species has a low probability of occurrence in the ecotone in any individual slope, but as the analytical expression of this model indicates, the probability of nonoccurrence of species declines rapidly as slopes (replicates) are added to the data set. In our landscape scale study, species richness in this zone is inflated by a large number of species with low abundances. Temperate species contribute maximally to richness (occurring in small numbers), but a very large number of tropical individuals are also found in this zone with no apparent contribution to overall richness (M. Oommen, *unpublished data*). At larger spatial scales, the richness peak in the primary (tropical–temperate) ecotone has a large number of species at their range limits (Fig. 2b). This is suggestive of successive accumulation of low abundance species across a number of local gradients.

Based on the analyses of overall richness patterns, patterns within biogeographic groups, and species dynamics at ecotones, we speculate that though unimodal richness patterns may be the norm, on the rare occasion when gradients are extensive at small spatial scales, bimodal or multimodal patterns could arise as a result of the inclusion of two or more distinct biomes with very low overlap (e.g., very extensive local gradients with both tropical and temperate communities). Monotonic patterns are likely to be characteristic of exceptionally strong environmental gradients (e.g., temperature for some taxa) along small local gradients comprising a single large domain (e.g., tropical mountain systems). To summarize, the position and magnitude of the peak(s) will be a function of the strength and width of the domain(s) (both in terms of resource gradients whether strong or weak/gentle or steep, as well as the spatial scale), and the number of local gradients considered.

Though there have been numerous calls in recent literature to look at macroecological diversity patterns in the context of multiple mechanisms and scales (Pimm and Brown 2004, Rahbek 2005), few studies have explicitly addressed this. In a recent review of elevational studies on the diversity of small mammals at multiple levels, McCain (2005) points to evidence for ‘‘a suite of interacting climatic, area and geometric factors,’’ indicating a multiplicity of mechanisms. We suggest that multiple correlated factors themselves can cause unimodal patterns in overall species richness. Our investigations on woody plant diversity in the Indian Western Himalaya support this premise and provide evidence for different mechanisms among spatial scales, and also within a single spatial scale and its biological subsets. In this study, we benefited from exploring patterns and mechanisms across hierarchical spatial scales. A combination of primary and secondary data complemented each other; data on species richness at the local scale proved central to understanding within-domain diversity in biogeographic groups, whereas large-scale secondary data was critical in understanding the pattern across spatial scales.

ACKNOWLEDGMENTS

We thank Rashid Raza for his contribution to data collection, discussions, and comments. R. K. Colwell and Ajith Kumar provided extensive comments; K. J. Gaston, W. Jetz, and J. Kerr gave critical comments on previous versions of the manuscript; J. Krishnaswamy helped with statistical issues. J. Nawani, Gyan Singh, Kalyan Singh, Birender Singh, Umed Singh, and the late Vikram Singh helped with field data collection. Field work was part of a WII-USFWS funded project. The Forest Departments of Uttar Pradesh and Uttaranchal provided permits and logistic support. M. A. O. also thanks V. B. Mathur, R. S. Chundawat, Q. Qureshi, D. Hunter, and B. C. Choudhury. K. S. was supported by ATREE during the preparation of the manuscript.

LITERATURE CITED

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology **85**:1771–1789.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology **58**:445–449.

Coley, P. D., and J. A. Barone. 1996. Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics **27**:305–335.

Colwell, R. K. 2000. Range model: a Monte Carlo simulation tool for assessing geometric constraints on species richness. 〈http://viceroy.eeb.uconn.edu/rangemodel〉

Colwell, R. K., and G. C. Hurtt. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. American Naturalist **144**:570–595.

Colwell, R. K., and D. C. Lees. 2000. The mid-domain effect: geometric constraints on the geography of species richness. Trends in Ecology and Evolution **15**:70–76.

Colwell, R. K., C. Rahbek, and N. J. Gotelli. 2004. The mid-domain effect and species richness patterns: what have we learned so far? American Naturalist **163**:E1–E23.

Grytnes, J. A. 2003. Species-richness patterns of vascular plants along seven altitudinal transects in Norway. Ecography **26**:291–300.

Grytnes, J. A., and O. R. Vetaas. 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. American Naturalist **159**:294–304.

Lomolino, M. V. 2001. Elevation gradients of species-density: historical and prospective views. Global Ecology and Biogeography **10**:3–13.

Lyons, S. K., and M. R. Willig. 1997. Latitudinal patterns of range size: methodological concerns and empirical evaluation for New World bats and marsupials. Oikos **79**:568–580.

McCain, C. M. 2005. Elevational gradients in diversity of small mammals. Ecology **86**:366–372.

Patterson, B. D., D. F. Stotz, S. Solari, J. W. Fitzpatrick, and V. Pacheco. 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. Journal of Biogeography **25**:593–607.

Pimm, S. L., and J. H. Brown. 2004. Domains of diversity. Science **304**:831–833.

Rahbek, C. 1995. The elevational gradient in species richness: a uniform pattern? Ecography **18**:200–205.

Rahbek, C. 1997. The relationship among area, elevation, and regional species richness in neotropical birds. American Naturalist **149**:875–902.

Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species richness patterns. Ecology Letters **8**:224–239.

Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Shmida, A., and M. W. Wilson. 1985. Biological determinants of species diversity. Journal of Biogeography **12**:1–20.

Singh, J. S., and S. P. Singh. 1992. Forests of Himalaya: structure, functioning and impact of man. Gyanodaya Prakashan, Naini Tal, India.

Singh, S. P., B. S. Adhikari, and D. Zobel. 1994. Biomass, productivity, leaf longevity, and forest structure in the Central Himalaya. Ecological Monographs **64**:401–421.

S-PLUS. 2000. Professional Release 1. Version 4.5. Copyright 1988–1999. MathSoft. Seattle, Washington, USA.

Stevens, G. C. 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. American Naturalist **140**:893–911.

Storch, D., and K. J. Gaston. 2004. Untangling ecological complexity on different scales of space and time. Basic and Applied Ecology **5**:389–400.

Storch, D., P. A. Marquet, and K. J. Gaston. 2005. Untangling an entangled bank. Science **307**:684–686.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs **30**:279–338.

APPENDIX A

A list of literature sources for secondary data on woody plant distribution in the Indian Western Himalaya is available in ESA's Electronic Data Archive: *Ecological Archives* E086-165-A1.

APPENDIX B

Correlates of species richness for different biogeographic groups at the landscape scale, based on evaluation of regression models for 100-m class analysis, are reported in ESA's Electronic Data Archive: *Ecological Archives* E086-165-A2.

APPENDIX C

Correlates of species richness for different biogeographic groups at the landscape scale, based on evaluation of regression models for 200-m class analysis, are reported in ESA's Electronic Data Archive: *Ecological Archives* E086-165-A3.

APPENDIX D

Details of the ecotone accumulation model to demonstrate effect of scale on species richness patterns are available in ESA's Electronic Data Archive: *Ecological Archives* E086-165-A4.