

10 Diverse Elevational Diversity Gradients in Great Smoky Mountains National Park, U.S.A.

Nathan J. Sanders, Robert R. Dunn, Matthew C. Fitzpatrick, Christopher E. Carlton, Michael R. Pogue, Charles R. Parker, and Theodore R. Simons

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INTRODUCTION

“To do science is to search for repeated patterns. . . .”

—**Robert MacArthur, 1972**

Why does the number of species vary geographically? The earliest naturalists puzzled over this question (von Humboldt, 1808), as do many biogeographers and macroecologists today (Gaston, 2000; Hawkins et al., 2003; Currie et al., 2004). Over the last 200-plus years, the most striking geographic pattern in species richness—the decline in species richness with increasing latitude—has received the most attention (e.g., Hillebrand, 2004). Thanks to many recent theoretical developments (Colwell et al., 2004), coupled with global-scale databases (e.g., Kreft and Jetz 2007; Jetz et al., 2007; <http://www.gbif.org>)

and satellite technology, the number of candidate mechanisms that shape the latitudinal diversity gradient has been whittled down to a manageable number (Hillebrand, 2004).

Less well-studied, however, are the factors that shape elevational diversity gradients. Because many climatic factors vary systematically along elevational gradients, as they might along latitudinal gradients, elevational diversity gradients were thought to be miniature versions of latitudinal gradients (Körner, 2000). For example, Brown (1988) wrote, “Just as change of physical conditions with altitude resembles in many respects the variation with latitude, so the decreasing diversity of most organisms with increasing elevation mirrors in most respects the latitudinal gradient of species richness.” Stevens (1992) noted that, “Biologists have long recognized that elevational and

latitudinal species-richness gradients mirror each other.” Although the most common relationship between latitude and richness is a decline in diversity with increasing latitude, this is not the most common pattern along elevational gradients. Rahbek’s (1995; 2005) thorough reviews of published studies on elevational gradients showed that mid-elevation peaks in diversity are the norm. This suggests that elevational gradients do not mirror latitudinal gradients.

Rahbek’s (1995; 2005) approach to assessing how diversity varies with elevation was to count the number of published studies that showed monotonic decreasing, hump-shaped, flat-horizontal, then decreasing, increasing, or some other relationship between richness and elevation. The studies that he compiled were from various mountain ranges, and on various taxa. One reason that different patterns of elevational diversity might occur in different systems is because the scale and extent of the elevational gradients varied among studies (Rahbek, 2005) or because different mountain ranges are embedded in different regional climatic areas with different evolutionary histories.

Another approach to understand how diversity varies with elevation is to analyze the patterns of diversity for several taxa along the same elevational gradient (Pausas, 1994; Pharo et al., 1999; Kessler, 2000; Grytnes et al., 2006). Such analyses are relatively rare in the literature, perhaps because they require synthesizing multiple electronic databases. Clearly, understanding whether many taxa respond to elevation in the same ways will help uncover the underlying mechanisms. Of course, diversity does not respond to latitude or elevation per se; latitude and elevation are only surrogates for a variety of factors that shape diversity gradients (Körner, 2007). For example, both climate and area affect diversity (e.g., Currie et al., 2004; Rosenzweig et al., 1995) and vary along elevational gradients (Rahbek, 2005; Romdal and Grytnes, 2007). The strengths of examining diversity gradients for several taxa along the same elevational gradient are that (1) one can control for different environmental histories and regional factors that often exist among different mountain ranges, and (2) climatic data are often easier to obtain along a single gradient than along many gradients dispersed throughout the world. Moreover, because the factors that lead to variation in species richness may differ among taxa, comparing elevational diversity gradients across taxa may provide useful insights about the factors that shape diversity gradients more generally.

In this study, we examine elevational gradients in diversity for several taxa along a single elevational diversity gradient in Great Smoky Mountains National Park

(GSMNP) in the southern Appalachians of the southeastern United States. This is a unique montane ecosystem for several reasons. First, there is a long and storied history of ecological and biodiversity research in GSMNP, going back more than seventy years (e.g., Whittaker, 1952; Whittaker, 1956). Second, GSMNP is one of the most well-surveyed national parks in the United States. And third, since the mid-1990s, GSMNP has hosted an All-Taxa Biodiversity Inventory (ATBI) that aims to catalog the diversity of all life in the park (Sharkey, 2001; <http://www.discoverlife.org>), and much of the data from the ATBI are freely available online for investigators to mine. Therefore, it is possible to assess diversity gradients, and their potential underlying causes, for a variety of taxa. Here, we focus on elevational diversity gradients in ants, noctuid moths, breeding birds, and beetles. In addition, eleven sites were installed for a “pilot study” to understand better how to systematically sample biodiversity. From those eleven sites, we compare diversity gradients of spiders, beetles, flies, bugs, hymenopterans, and orthopterans. Specifically, we asked three questions: (1) Do different taxa exhibit different relationships between elevation and diversity in GSMNP? (2) Does area, climatic factors, or habitat diversity account for most of the variation in species richness? and (3) Does their relative effect (importance?) vary among taxa?

METHODS

STUDY AREA

GSMNP (area = 2,111 km²) is located in the southern Appalachian Mountains on the border of Tennessee and North Carolina, U.S.A. Elevation ranges from 270 m to 2,025 m. Approximately 95% of GSMNP is at least partially forested, and because of the extensive elevational gradient, many different forest types are found in the park, including some of the largest tracts of primary forest in the eastern U.S.A. The high elevation forests are not entirely evergreen—in some areas Northern red oak, buckeye-yellow birch, and beech associations are common.

PATTERNS OF DIVERSITY

The data we analyze here were collected in a variety of ways. Below, we summarize the sampling techniques for each taxon and for the “pilot study.” Importantly, we did not interpolate species richness by assuming that species were present in all elevational zones between the highest and lowest elevations at which they were collected (e.g., Grytnes and Vetaas, 2002; Grau et al., 2007), because this

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can inflate the signal of a mid-elevation peak in diversity when it might not actually exist.

Ants: Sanders et al. have sampled ants at twenty-nine forested sites ranging in elevation from 379 m to 1,828 m (Sanders et al., 2007; Lessard et al., 2007; Geraghty et al., 2007). The sites were all in mixed hardwood forests and located in areas away from roads, heavily visited trails, or other recent human disturbances. At each site, a 50 m × 50 m plot was placed, and we sampled ants in sixteen 1 m² quadrats within each site. Within each 1 m² quadrat, we collected the leaf litter and sifted it through a coarse mesh screen of 1 cm grid size to remove the largest fragments and concentrate the fine litter. The litter fragments that did not fit through the mesh, twigs and sticks, in each 1 m² quadrat were inspected for colonies. The concentrated fine litter from each of the sixteen 1 m² quadrats was then suspended in mini-Winkler sacks for two days in the laboratory. All worker ants that were extracted from the 1 m² quadrats were identified, enumerated, and stored in N. Sanders's ant collection at the University of Tennessee. A species list is available from N. Sanders. For more details of the sampling design, see Sanders et al., 2007, and Lessard et al., 2007.

Noctuid moths: Pogue et al. have sampled noctuid moths during 202 sampling bouts at 121 sites ranging in elevation from 305 m to 2,024 m in elevation. A variety of habitat types were sampled, including cove hardwood forests and old fields at low elevations, pine–oak and northern hardwood forests at mid-elevations, heath balds at mid- and high elevations, and spruce–fir forests at the highest elevations. At each site, a 15 w UV bulb attached to a box-type trap, and various types of UV or mercury vapor light, either in bucket-type traps or against a white sheet, was used to sample moths (Pogue, 2005, 2006). Sites were sampled at different times of year from 2001–2005 to capture phenological shifts in the moth fauna. We divided the elevational gradient into sixteen 100 m bands and combined the samples from all of the sites within each elevational band, as is common in many elevational diversity gradient studies (Rahbek, 2005). Observed species richness is the number of species collected within 100 m elevational bands.

This study follows the recent classification of the Noctuidae, in which the former families Pantheidae, Lymantriidae, Noliade, and Arctiidae, (Kitching and Rawlins, 1999) are treated as subfamilies, making the Noctuidae easily defined and monophyletic (Lafontaine and Fibiger, 2006). Specimens were identified to species, and voucher specimens are stored at the U.S. National Museum, Smithsonian Institution, Washington, D.C.

Beetles: Species analyzed for this study were a subset of approximately 2,300 species currently recorded from GSMNP based on modern and historical records (Carlton and Bayless, 2007; complete checklist posted at <http://entomology.lsu.edu/lam/smokybeetles.htm>). The beetle fraction analyzed here was obtained from the eleven pilot study sites, mainly from Malaise trap samples, and from collections using a diversity of methods by the team from the Louisiana State Arthropod Museum and cooperators within the beetle twig of the ATBI during 2001–2006. A large proportion of specimens were derived from forest litter sampling from seventy-two localities across the entire range of GSMNP elevations and forest types. Those samples typically consisted of 2–5 kg of litter that had been sifted through 0.8 cm mesh wire screen. Specimens were extracted using standard Berlese funnel techniques (e.g., Carlton and Robison, 1998). Additional methods employed during the same time frame included flight intercept trapping, pitfalls, light traps, and hand collecting from vegetation, dead wood, under rocks, and fungi. Specimens were identified to species or genus, and sorted to morphospecies (for taxonomically intractable taxa). Vouchers are divided between the Louisiana State Arthropod Museum and the GSMNP collection.

Breeding birds: Simons et al. conducted 7,535 variable circular plot point transects (Reynolds et al., 1980) at 4,157 point locations from mid-May to the end of June in GSMNP (Shriner, 2001; Shriner et al., 2002; Simons et al., 2006). Points were established ~250 m from one another, mostly along low-use hiking trails. However, some points were located along roads with little traffic and along off-trail transects. At each point location, all of the birds seen or heard within 10 minutes were recorded. Observed species richness is the number of species detected within 100 m elevational bands. Birds present unique problems, which many of the other taxa in this study do not. Namely, detection probability can differ drastically among species, nocturnal birds are generally not sampled, and altitudinal migrants pose other problems as well. However, we note that many such studies of patterns of bird diversity, across spatial scales, suffer from the same shortcomings.

The “pilot study”: Between January 1999 and 2002, C. Parker organized the structured sampling of arthropod biodiversity at eleven sites ranging in elevation from 521 m to 1,944 m. At each site, ten pitfall traps were placed ~3 m apart along an approximately 30 m long transect. The pitfall traps were 6 cm diameter cups buried flush with the soil surface and were collected every two weeks. At the same sites, two Malaise traps were placed on the ground 75–100 m from one another, and

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the contents of the traps were collected every two weeks from January 1999 to January 2002. For the pilot study, observed species richness is the number of species collected at each site from 1999–2002.

UNDERLYING CAUSES OF DIVERSITY GRADIENTS

We asked how three factors might influence patterns of diversity across taxa in this system: actual evapotranspiration (AET), area, and habitat diversity. To estimate AET, we obtained temperature and precipitation data for GSMNP from the WorldClim 1.4 database (Hijmans et al., 2005). Though many environmental data are available, we limited the number of variables used here to AET because we wanted to minimize the number of collinear variables in subsequent analyses and because AET is an important correlate of diversity at broad spatial scales (Currie et al., 2004). We estimated AET based on Turc's formula (Turc, 1954; Kluge et al., 2006), where $AET = P/[0.9 + (P/L)^2]^{1/2}$ with $L = 300 + 25T + 0.05T^3$, P = annual mean precipitation, and T = mean annual temperature. AET is strongly related to net primary productivity ($r^2 = 0.93$), but the relationship is nonlinear (Kaspari et al., 2000).

To estimate area in each elevational band, we used a 30 m resolution digital elevation model of GSMNP to estimate the area of each elevational band from 400 m to > 1,900 m.

We estimated habitat diversity as the number of different habitat types in each 100 m elevational band by combining a 30 m resolution digital elevation model with a vegetation map of the GSMNP. The map was created in 2004 and is based upon 1:12,000 color-IR photography. The minimum mapping unit is 0.5 ha. The accuracy assessment indicated that the classifications were 80% accurate (Michael Jenkins and Ed Laurent, *personal communication*).

Statistical analyses. In addition to examining patterns in observed species richness, S , with elevation, we also calculated Fisher's α , a widely used estimate of diversity that is independent of sample size (Evans et al., 2005). Fisher's α also removes the sampling effect (i.e., the fact that diversity might be high at a site simply because there are more individuals at that site). We first related S and Fisher's α at each site (for the ants and for the species from the "pilot study") or in each elevational band by regressing both S and Fisher's α against elevation. For each richness-elevation plot, we asked whether a linear or polynomial regression best captured the relationship between richness and elevation. For the "pilot study" data, we tested for taxonomic covariance using pair-wise correlations among taxa.

To examine some potential factors which may shape variation in richness of ants, noctuid moths, beetles, and breeding birds along the elevational gradient, we used forward stepwise regression (P to enter < 0.10) to test whether AET, AET^2 , area, or habitat diversity within the elevational band accounted for most of the variation in S and Fisher's α for each set of taxa. AET^2 accounts for potential curvilinear relationships between diversity and AET. For each taxon, we used AIC scores to determine the best model for each elevational diversity gradient. Owing to limited sample sizes ($n = 11$), we did not explore the potential underlying causes of the diversity from the pilot study.

RESULTS

PATTERNS OF DIVERSITY

Ants: We collected forty-one species of ants in forested ecosystems in GSMNP. Ant species richness declined linearly with elevation ($r^2 = 0.59$, $P < 0.0001$; Figure 10.1a). Fisher's α also declined linearly with elevation ($r^2 = 0.63$, $P < 0.0001$; Figure 10.2a).

Noctuid moths: In total, we collected 11,322 individuals and 517 species of noctuid moths. Observed species richness declined with elevation (quadratic regression: $r^2 = 0.51$, $P = 0.01$; Figure 10.1b), but leveled off at the highest elevations (above 1,500 meters). Fisher's α declined linearly with elevation ($r^2 = 0.60$, $P = 0.0004$; Figure 10.2b).

Beetles: We collected 847 species from a data set of 21,308 individuals. We note that hundreds of specimens have yet to be identified. Neither observed species richness nor Fisher's α varied systematically with elevation (Figure 10.1c, Figure 10.2c).

Breeding birds: In total, 65,489 individuals and 111 species were detected. Bird species richness exhibited a hump-shaped relationship with elevation, with richness peaking at 700 m. The diversity gradient was best described by a quadratic regression ($y = -0.0004x^2 + 0.0644x + 43.067$, $r^2 = 0.52$, $P = 0.005$; Figure 10.1d). This relationship was driven by two low-elevation, low diversity elevational bands. These two points were relatively under sampled and clustered around a few particular locations. If they are removed from the analysis, then richness decreases monotonically with increasing elevation ($r^2 = 0.78$, $P < 0.0001$). The relationship between Fisher's α and elevation also was best explained by a polynomial regression ($= -0.000002x^2 + 0.00007x + 13.34$, $r^2 = 0.77$, $P < 0.0001$; Figure 10.2d), with diversity

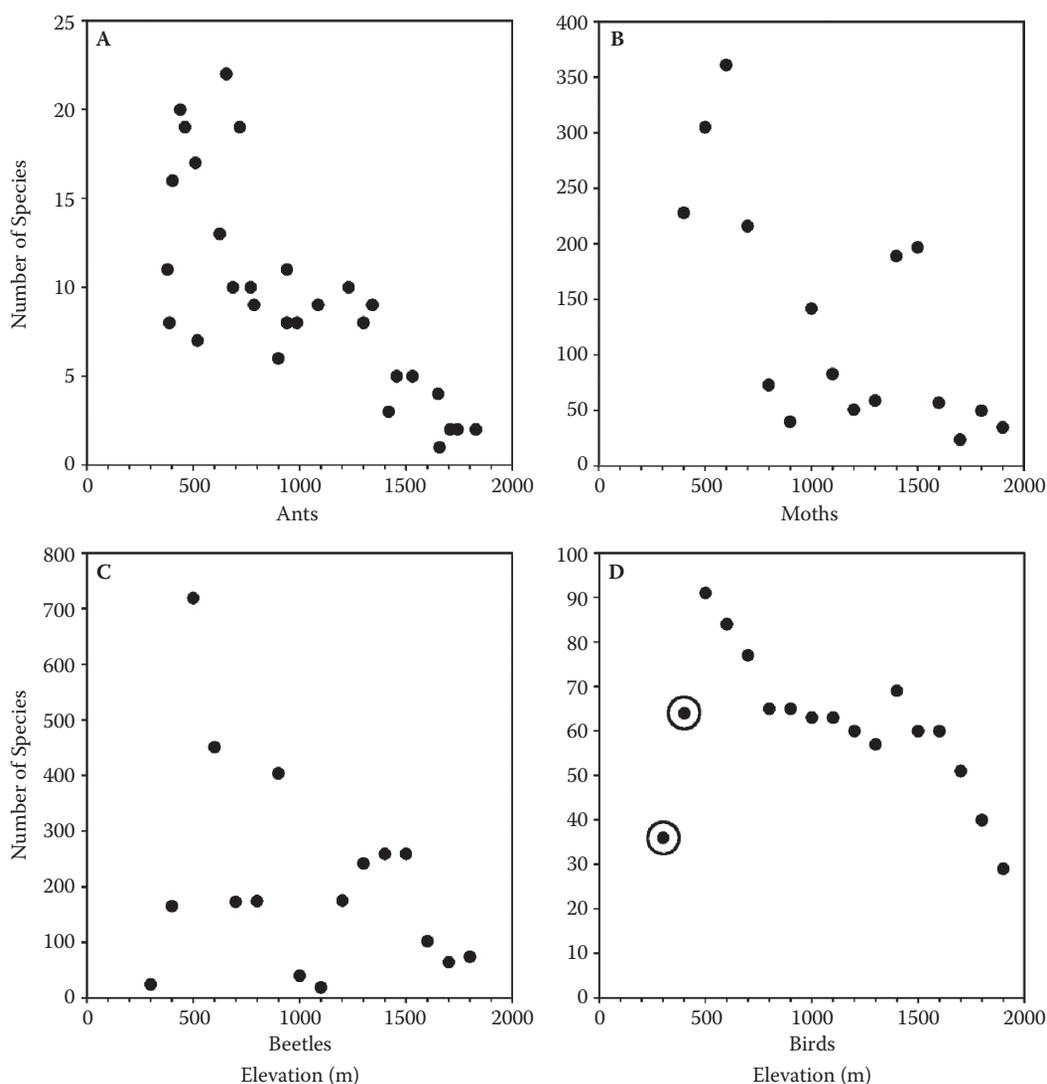


FIGURE 10.1 The relationship between species richness and elevation for ants at twenty-nine sites (a), noctuid moths in 100 m elevational bands (b), beetles in 100 m elevational bands (c), and birds in 100 m elevational bands (d) in Great Smoky Mountains National Park. In panel (d) the two circled data points indicate two low-elevation sites that were excluded from some analyses because they were not sampled as intensively as the other sites at higher elevations.

tending to be flat then declining at approximately 700 m. Again, however, we caution that the sampling was not designed to sample bird diversity, per se, and there are many confounding factors (e.g., variation in detection probability among species, altitudinal migrants, etc.) that we have glossed over in this manuscript.

The “pilot study”: Richness declined with elevation for the spiders, coleopterans, and orthopterans, but there was no relationship between richness and elevation for the dipterans, hemipterans, or hymenopterans (Figure 10.3). Fisher’s α , which corrects for sampling

effects, did not vary systematically for any of the taxa except the orthopterans. Fisher’s α of the orthopterans declined linearly with elevation ($r^2 = 0.65$, $P < 0.003$). Though the six arthropod taxa examined here exhibited different elevational diversity gradients, richness of several taxa covaried among sites (Table 10.1).

UNDERLYING CAUSES OF DIVERSITY GRADIENTS

AET declined monotonically with elevation ($r^2 = 0.93$, $P < 0.0001$), but the relationship between AET² and

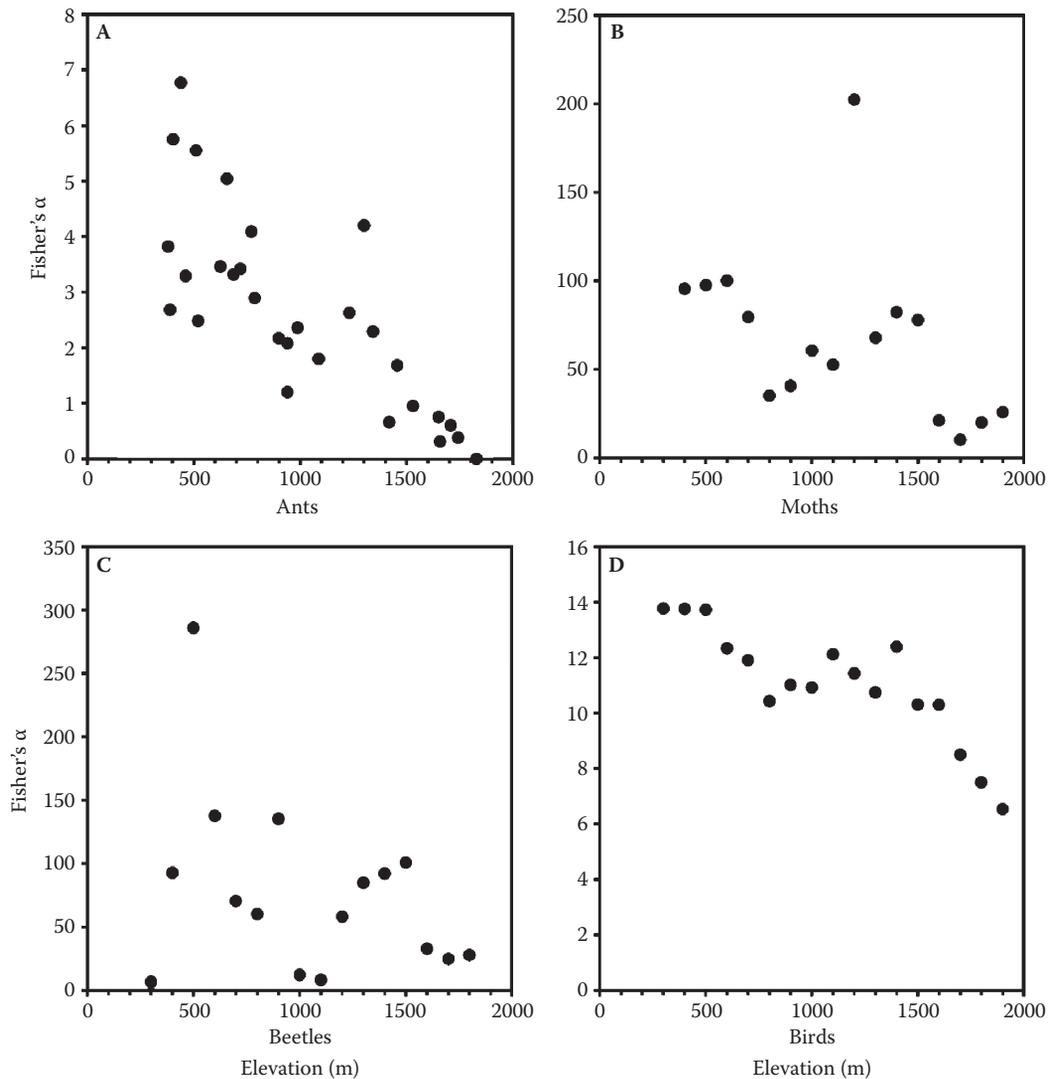


FIGURE 10.2 The relationship between Fisher's α diversity and elevation for ants at twenty-nine sites (a), noctuid moths in 100 m elevational bands (b), beetles in 100 m elevational bands (c), and birds in 100 m elevational bands (d) in Great Smoky Mountains National Park.

elevation was best described by a polynomial regression ($r^2 = 0.99$, $P < 0.0001$). The relationship between log-area of each elevational band and elevation was largely flat, then declined above 1,500 m ($r^2 = 0.94$, $P < 0.0001$). Habitat diversity was highest at low elevations, flat at mid-elevations, and then declined linearly above approximately 1,500 m. The relationship between habitat diversity and elevation was best described by a third order polynomial regression ($r^2 = 0.88$, $P < 0.0001$).

Ants: AET accounted for 60% of the variation in ant species richness (Table 10.2), and no other factor entered the stepwise regression model. Similarly, AET alone

accounted for most of the variation in Fisher's α diversity of ants (Table 10.3).

Noctuid moths: Only AET² accounted for variation in noctuid moth richness, suggesting that the relationship between the richness of noctuid moths and AET is hump-shaped (Table 10.2). However, when we corrected for variation in moth abundance by using Fisher's α , only the number of habitats accounted for variation in moth diversity (Table 10.3).

Beetles: AET alone accounted for 27% of the variation in the number of beetle species (Table 10.2). However, correcting for variation in the number of individuals by

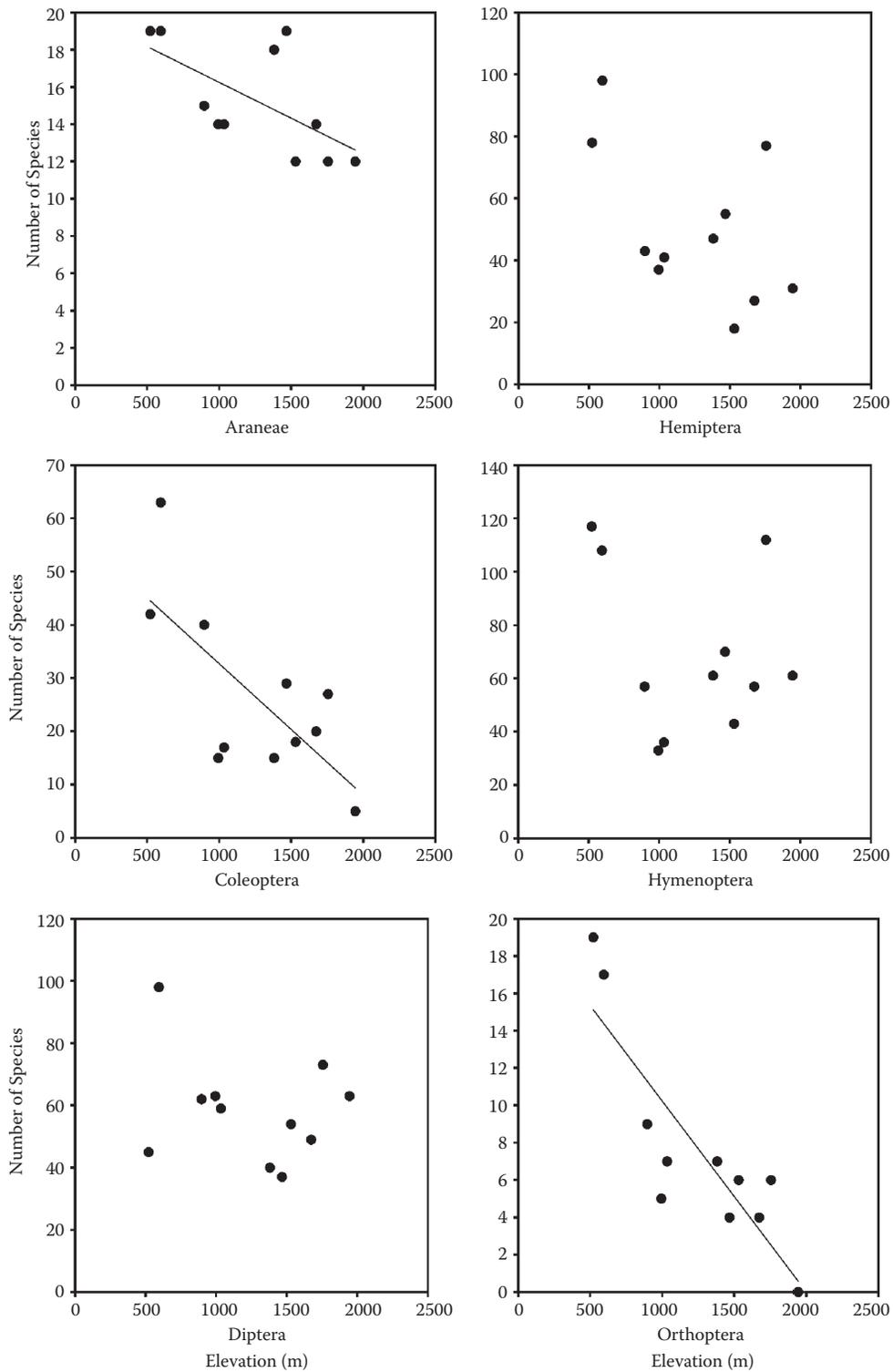


FIGURE 10.3 Results from the ATBI “pilot study.” In each panel, the number of species collected at eleven sites over two years is displayed for that particular taxon. The line (where displayed) is the best-fit linear regression line. If no line is present, then the relationship was not statistically significant.

TABLE 10.1
Correlation Matrix for Six Arthropod Taxa Collected at Eleven Sites as Part of the All Taxa Biodiversity Inventory 'Pilot Study' in Great Smoky Mountains National Park

	Coleoptera	Diptera	Hemiptera	Hymenoptera	Orthoptera
Araneae	0.62	-0.15	0.60	0.43	0.64
Coleoptera		0.50	0.80	0.67	0.84
Diptera			0.49	0.31	0.29
Hemiptera				0.87	0.74
Hymenoptera					0.64

Note: Values in the matrix are Pearson correlation coefficients. Significant ($P < 0.05$) values are indicated in **bold**.

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TABLE 10.2
Results from Stepwise Regression Analysis of Log-Area, AET, AET², and Habitat Diversity on the Number of Species of Ants, Noctuid Moths, Beetles, and Birds in Great Smoky Mountains National Park

Taxon	Factor	Parameter	Partial r^2	P	Whole Model r^2	AIC
Ants	AET	0.036	0.60	< 0.0001	0.60	78.78
Moths	AET ²	0.0007	0.54	0.001	0.54	139.67
Beetles	AET	0.78	0.27	0.948	0.27	154.96
Birds	Log-Area	42.12	0.68	0.0001	0.94	50.89
	AET ²	0.0005	0.13	0.0009		
	No. of habitats	-1.20	0.09	0.005		
	AET	-0.39	0.03	0.03		

TABLE 10.3
Results from Stepwise Regression Analysis of Log-Area, AET, AET², and Habitat Diversity on Fisher's α Diversity of Ants, Noctuid Moths, Beetles, and Birds in Great Smoky Mountains National Park

Taxon	Factor	Parameter	Partial r^2	P	Whole Model r^2	AIC
Ants	AET	0.011	0.63	< 0.0001	0.63	6.64
Moths	No. of habitats	3.39	0.36	-0.01	0.36	118.83
Beetles	AET	0.0004	0.33	-0.02	0.33	124.3
Birds	No. of habitats	0.15	0.75	< 0.0001	0.83	-1.26
	AET ²	0.0006	0.83	0.02		

using Fisher's α indicates that the relationship between beetle diversity and AET is hump-shaped ($r^2 = 0.33$) because only AET² entered the model (Table 10.3).

Breeding birds: AET (partial $r^2 = 0.63$) and area (partial $r^2 = 0.11$) accounted for most of the variation in the number of bird species along the gradient (Table 10.2). If

we remove the two low elevation, low diversity sites from the analysis, AET (partial $r^2 = 0.78$) and area (partial $r^2 = 0.08$) account for most of the variation in the number of bird species along the gradient. However, habitat diversity and AET² together accounted for 83% of the variation in Fisher's α diversity of birds (Table 10.3).

DISCUSSION

Our results show that patterns of species richness of a variety of taxa differ along the same elevational gradient, though AET seems to be an important correlate of diversity in this system, because AET and the focal organisms in this study respond to similar climatic drivers. Only because multiple investigators provided data to a single database was it possible to test whether the drivers of diversity were the same across taxa in this montane ecosystem. Other databases for montane ecosystems likely exist, and could be easily mined by others as a test of the generality of the patterns and their underlying causes we describe here.

Here, we first discuss the patterns of richness and taxonomic covariance along this elevational gradient. Then we move on to consider the underlying causes of the patterns.

PATTERNS OF DIVERSITY

A common pattern in studies of elevational diversity gradients is that diversity either declines with elevation or peaks at mid-elevations (Rahbek, 2005). We document similar patterns here: richness of ants and moths tended to decline with increasing elevation, but birds exhibited a mid-elevation peak in diversity, though with a peak near the base of the gradient. Beetles, however, exhibited no strong pattern in diversity along the elevational gradient. Other studies that have examined multiple taxa along a common elevational gradient also have found variation in diversity patterns among taxa (Pausas, 1994; Pharo et al., 1999; Kessler, 2000; Bhattarai and Vetaas, 2003; Grau et al., 2007). Interestingly, most of these studies focused solely on plants. To our knowledge, ours is one of the first to explore patterns of diversity for multiple animal taxa along the same elevational gradient.

Not surprisingly, species richness of ants declines with elevation. Most studies on elevational gradients in ant diversity have found that ant species decrease with elevation (Sanders et al., 2007; Lessard et al., 2007) or, less frequently, peak at mid-elevations (Olson, 1991; Fisher, 1996; Fisher, 1998; Samson et al. 1997; Brühl et al., 1999; Sanders et al., 2003). Of those studies that found a peak in ant species richness, the peak occurred at elevations below the maximum elevation used in this study (Samson et al., 1997; Fisher, 1998).

The diversity of noctuid moths declined with elevation in this study, as in an earlier analysis of the same data (Sanders et al., in review). Of the other studies that have

examined patterns in moth diversity along elevational gradients, nearly every conceivable pattern has been documented. For instance, the diversity of geometrid moths does not vary with elevation in the Andes (Brehm et al., 2003), or in tropical forests in Borneo (Schulze, 2000), or along Mt. Kilimanjaro (Axmacher et al., 2004). Similarly, the diversity of arctiid moths also is moderately constant along an elevational gradient in Borneo (Holloway, 1987). In contrast, diversity of geometrid moths along the Barva Transect in Costa Rica peaks at mid-elevations (Brehm et al., 2007). But our results here are that diversity declines nearly linearly with elevation. Of course, it could be the case that the patterns differ, but the underlying mechanisms are the same among studies, a subject to which we will return.

It is somewhat surprising that beetle diversity showed no pattern along the gradient. Most studies to date on elevational diversity gradients in beetles have focused on dung beetles (e.g., Escobar et al., 2005, and references therein), and the general pattern is that beetle diversity declines with elevation. So why is there no elevational diversity gradient for beetles in GSMNP? We can think of two reasons. First, we are ignoring a tremendous amount of trophic diversity by lumping all 847 species. It could be the case that the scarabs or the weevils or the chrysomelids alone decline with elevation. However, such an analysis is beyond the scope of this chapter. Second, though there is no strong elevational pattern, beetles at least weakly track variation in AET, suggesting that climatic variation along the elevational gradient, rather than elevational, *per se*, influences spatial variation in beetle diversity.

Bird diversity peaked at low-elevations in GSMNP. In a series of landmark studies on elevational diversity gradients in tropical birds, Terborgh (1971, 1977, 1985), and later Rahbek (1997), documented complex patterns of bird diversity along elevational gradients in the Andes. Terborgh's observations indicated that bird species richness declined monotonically with elevation, but when he corrected for sampling effort, the pattern was markedly hump-shaped, with a peak at mid-elevations. Similarly, Rahbek (1997) found monotonic decreases in diversity with elevation, but when he factored out the effect of area within each band, the pattern became hump-shaped. Kattan and Franco (2004) also found that diversity declined monotonically along an elevational gradient in the Andes. In our study in the southern Appalachians, the elevational diversity gradient is linear when we correct for sampling deficiencies at the lowest elevations.

Even when specifics of the diversity patterns differ among taxa, those patterns can still share common features. For example, across taxa, the peaks in diversity tended to be at approximately 500–600 m in elevation, the bottom or near to the bottom of our elevational gradient. In addition, the data from the “pilot study” indicate some degree of taxonomic covariance (e.g., Lamoreux et al., 2005). Gaston (2000) noted that the “lack of strong positive covariance in the species richness of higher taxa is significant in that it constrains the extent to which observed patterns in biodiversity can be extrapolated from one group to another, and from exemplar groups to biodiversity at large.” Here, however, there is some suggestion that diversities are correlated among taxa. For example, coleopterans, orthopterans, hymenopterans, and hemipterans tend to covary with one another at the eleven sites sampled by Parker et al. during the pilot study. Practically speaking, this suggests that sampling one taxon, for example, the coleopterans, might be representative of the diversity of other taxa.

In this study, taxa from the pilot study covary; peaks in diversity along the elevational gradient for ants, birds, beetles, and noctuid moths are mostly congruent, but the elevational diversity patterns of the ants, birds, beetles, and moths do not necessarily mirror one another. For example, beetles and other taxa were correlated in richness in the pilot samples but not in our broader analyses of birds, ants, moths and beetles. How could this be? There are two possibilities. First, taxonomic covariance at small spatial scales tends to be more common than taxonomic covariance at large spatial scales (Gaston 2000; but see Lamoreux et al., 2005). Particular sites within the eleven sites for the pilot study might be amenable to diverse taxa. But once scale increases to encompass 100 m elevational bands, then more habitat heterogeneity is introduced, as is variation in sampling completeness for the taxa of interest. Second, though the elevational diversity patterns at large scales might not be entirely congruent with one another, the underlying mechanisms shaping the patterns could be. This is the topic we turn to now.

UNDERLYING CAUSES OF DIVERSITY GRADIENTS

For the ants, beetles, moths, and birds, actual evapotranspiration accounted for at least a portion of the variation in species richness along the elevational gradient. However, the relationship between AET and richness varied among taxa. For example, the relationship between moth diversity and AET was hump-shaped, but ant, beetle, and bird diversity were all monotonically related to AET. There is a substantial body of literature about why energy

availability and diversity should be correlated (e.g., see Clarke and Gaston, 2006, and Currie et al., 2004 for a review). Further, because AET and temperature are highly correlated in GSMNP (because rainfall is relatively invariant), we also can not rule out mechanisms that involve temperature. AET is a strong correlate of energy availability and integrates over other factors that might influence diversity, such as season length, ambient humidity, and soil moisture. However, obtaining data on those factors, and how the focal organisms respond to them, proved beyond the scope of this study.

Along elevational gradients, the most plausible explanation is probably a “more individuals” mechanism (Kaspari et al., 2000), which posits that areas with more energy support larger populations and because populations are larger, extinction probabilities are reduced. As a result, areas with more energy have more species, simply because more individuals are supported. In the southern Appalachians, areas with higher temperature, and hence higher AET, do tend to have more individuals (of ants; Sanders et al., 2007), and sites with more individuals tend to have more species. However, other mechanisms above and beyond a “more individuals” mechanism must operate in this system because the relationship between bird and moth diversity and AET is hump-shaped. Moreover, bird diversity is best accounted for by area of each elevational band, which is common in other studies of bird diversity as well (Rahbek, 1997). Finally, area, the number of habitats, and AET all affect diversity above and beyond their effects on the number of individuals. When we correct for variation in the number of individuals by using Fisher’s α , AET still accounts for the largest portion of the variation in ant and beetle diversity, but not moth and bird diversity.

Taken together, the results from our study suggest that the factors that influence elevational diversity gradients, at least for ants, moths, beetles, and birds in this system, need not be the same among taxa or affect diverse taxa in similar ways. A substantial portion of biogeographical and macroecological research has sought to elucidate the single (or handful) of mechanisms that shape broad-scale diversity patterns (e.g., Allen et al., 2002, but see Hawkins et al., 2007). But our results suggest that even along the same elevational gradient, neither patterns nor mechanisms are entirely congruent. MacArthur (1972) famously noted that, “To do science is to search for repeated patterns,” but, at least in this system and in others (e.g., Grytnes et al., 2003), repeated patterns might be the exception rather than the rule. Only by mining the numerous data sets on montane biodiversity that are rapidly becoming available might ecologists come closer to

understanding the general patterns (if such patterns exist) and underlying causes of elevational diversity gradients.

SUMMARY

To understand how diversity varies with elevation, a good approach is to analyze the patterns of diversity for several taxa along the same elevational gradient. Such analyses are rare, as they require synthesizing multiple electronic databases. In our study, we analyze patterns of diversity along the same elevational gradient in Great Smoky Mountains National Park (GSMNP) in the southern Appalachians (U.S.A.) for many different taxa (ants, noctuid moths, breeding birds, and beetles). GSMNP is one of the most well-surveyed national parks, with a long history and effort to catalogue the diversity of all life in the park (All-Taxa Biodiversity Inventory). Peaks in diversity along the elevational gradient are mostly congruent between the four groups of taxa studied, but elevational diversity patterns differ, and each taxon group responded to environmental variation in different ways. Particularly, actual evapotranspiration (AET) accounted for a large portion of variation in all four groups of taxa, and area and number of habitats accounted for another portion of variation. Our results suggest that even along the same elevational gradient, neither patterns nor mechanisms are entirely congruent, so at least in this system, repeated patterns are the exception rather than the rule.

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