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Spatial Grain and the Causes of Regional Diversity Gradients in Ants

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abstract: Gradients of species richness (S; the number of species of a given taxon in a given area and time) are ubiquitous. A key goal in ecology is to understand whether and how the many processes that generate these gradients act at different spatial scales. Here we evaluate six hypotheses for diversity gradients with 49 New World ant communities, from tundra to rain forest. We contrast their performance at three spatial grains from S_{plot}, the average number of ant species nesting in a m^2 plot, through Fisher's α, an index that treats our 30 1-m^2 plots as subsamples of a locality's diversity. At the smallest grain, S_{plot} was tightly correlated ($r^2 = 0.99$) with colony abundance in a fashion indistinguishable from the packing of randomly selected individuals into a fixed space. As spatial grain increased, the coaction of two factors linked to high net rates of diversification—warm temperatures and large areas of uniform climate—accounted for 75% of the variation in Fisher's α. However, the mechanisms underlying these correlations (i.e., precisely how temperature and area shape the balance of speciation to extinction) remain elusive.

Keywords: ants, area, biodiversity, speciation, temperature, spatial scale.

Species richness, S, is the number of species of a given taxon in a given area and time (e.g., *Dipodomys* ha^{-1} yr^{-1}, Formicidae m^{-2} d^{-1}). If we hold two of these three descriptors constant, gradients of S can vary in interesting ways as we scale up in time (e.g., How many species of bees will pollinate a tree in a given year versus its 200-yr life span [Rosenzweig 1995]?) and scale up taxonomically (What are the rules that govern the richness of *Asclepias* versus all angiosperms [O'Brien et al. 1998; Kaspari 2001]?). Gradients in S also occur at every spatial scale studied by biologists, from the 1-cm cores of the protozoologist (Fenchel 1992) to the 1-m^2 plots used by experimental plant ecologists (Kareiva and Andersen 1988) to the 1° × 1° grids favored by macroecologists (Ricklefs 1987; Rosenzweig 1995; Crawley and Harral 2001). Thus, ecologists do not just grapple with the rules regulating S for a given taxon at a given time and place. They ultimately want to know how these rules scale. Here we address both questions by asking the following: How do the processes that limit ant species richness scale up with the size of the area sampled?

We focus on ants because they are easily sampled with quadrats (Agosti et al. 2000; Kaspari et al. 2000*a*), are diverse but with a well-developed α taxonomy, and are common in virtually every terrestrial habitat from tundra to rain forest (Holldobler and Wilson 1990; Kaspari et al. 2000*b*). Given their varied roles as predators, scavengers, seed dispersers, and competitors (Tilman 1978; Franks 1982; Beattie 1985; Cushman and Whitham 1991; Levey and Byrne 1993) and their impact as invasive species (Ward 1987; Porter 1988; Human and Gordon 1997; Holway 1998; Gotelli and Arnett 2000; Kaspari 2000), changes in ant diversity should have ramifications throughout the ecosystem.

We study 49 New World localities arrayed along the terrestrial plant productivity gradient (Kaspari et al. 2000*b*); all but two of our samples come from North and Central America (fig. 1). Using the terminology of Scheiner et al. (2000), we identify the extent (the distance between localities) as varying between approximately 1 km along an elevational gradient to hundreds of kilometers across the center of North and South America (fig. 1). We analyze patterns of diversity at three grains (the areas of our samples; see "Methods") that span two orders of magnitude but range within the size that most ecologists would call local.

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Six Hypotheses for the Regulation of Local Species Richness

How should the processes limiting S change as we increase grain? Species richness (S) changes proportional to the rate at which speciation, P, and migration, M, add species to the area, and extinction, X, removes the last individual of a species from an area (Ricklefs 1989; Huston 1994; Rosenzweig 1995; Hubbell 2001) such that

$$\frac{dS}{dt} = P + X + M.$$

Diversity hypotheses vary in the degree to which they treat P, X, and M as well as in how they incorporate, implicitly or explicitly, spatial grain (Elton 1927; Pianka 1966; Rhode 1992). Here we briefly summarize six of these hypotheses.

Sampling Hypothesis

A taxon, for a given area and time, can be characterized not only by S but also by N, the total number of individuals (May 1975); N in turn can increase as the average size of an individual decreases or as a habitat's productivity or time since disturbance increases (Huston 1994; Kaspari et al. 2000*a*). The sampling hypothesis is the first of two mechanisms we review through which gradients in N generate gradients in S.

Let S_A be the species richness in a plot of area A containing N_A individuals. This plot is embedded in a larger area, $A + 1$, which contains S_{A+1} species and N_{A+1} individuals; $S_A \leq N_A$ and $S_{A+1} \leq N_{A+1}$ by definition. The sampling hypothesis predicts the curve $S_A = f(N_A)$ within a pool of S_{A+1} species. It assumes that individuals are distributed randomly in space and that some species are more common than others. If so, then as N_A increases, S_A registers common species more rapidly than rare species (Preston 1962), producing a curve in which S_A is a positive decelerating function of N_A and is $\leq S_{A+1}$ (Preston 1962; Rosenzweig 1995; Gotelli and Colwell 2001; Hubbell 2001).

Abundance-Extinction Hypothesis

All assemblages are composed of taxa with nonzero probabilities of extinction. A population's probability of demographic extinction is a negative decelerating function of its population size (Leigh 1981; Pimm et al. 1988). Thus, for a given species abundance distribution, S is predicted to be a positive decelerating function of N, since high taxon abundance protects an area's species from demographic extinction (Levinton 1979; Hubbell and Foster 1986; Pimm et al. 1988; Kaspari et al. 2000*a*).

The sampling hypothesis and abundance-extinction hypothesis make the same prediction: a positive decelerating plot of S_A versus N_A. The first describes the way N determines how a quadrat "captures" available species; the second results from the way N governs the rate at which an assemblage simplifies as its component species drift to extinction. Two methods can help quantify the relative contributions of both mechanisms. First, when S and N are sampled at two or more grains, the species-abundance distribution at grain $A + 1$ can be randomly sampled to generate an expected mean S_A (Gotelli and Graves 1996). Second, a variety of methods and indices (e.g., jackknifing, Fisher's α) remove the sampling effect by answering the question, What is the estimated diversity of an area had subsampling gone to completion? (i.e., When has a plot completely sampled the species richness in the area in which it is embedded [Colwell and Coddington 1994]?). If such an estimate still generates a positive, decelerating S_A versus N_A plot, this supports the abundance-extinction hypothesis.

Mass-Effect Hypothesis

Immigration is one means of enhancing S. An isolated plot with low M may have fewer species than its resources and conditions can support (MacArthur and Wilson 1967; Tilman 1997). The mass-effect hypothesis (Schmida and Whittaker 1981; Schmida and Wilson 1985; Stevens 1992; Rahbek 1997) posits that species populations can reproduce in a limited number of habitats. These habitats are arrayed across a landscape. When populations in a given habitat broadcast propagules, some fall into adjacent suboptimal habitats where they may persist but fail to reproduce. Adjacent habitats thus subsidize an area's S, increasing diversity in the same way that source populations subsidize sink populations (sensu Pulliam and Danielson 1991). The mass-effect hypothesis operates at the spatial extents in which habitats are connected by dispersal. It predicts that increasing the number and proximity of adjoining habitats enhances S. Steep elevational gradients, with narrow bands of habitat arrayed up a mountainside, are an efficient means of enhancing the number of habitats in a given area (Merriam 1890; Whittaker 1952; Rahbek 1997). Our localities are embedded in landscapes that vary in slope from mountainsides to flat prairie. We test the prediction that localities will support more ant species when embedded in areas with a large range of elevation (Kerr and Packer 1997).

Middomain Hypothesis

Picture an island surrounded by barriers that rarely admit new species. The middomain hypothesis assumes that each

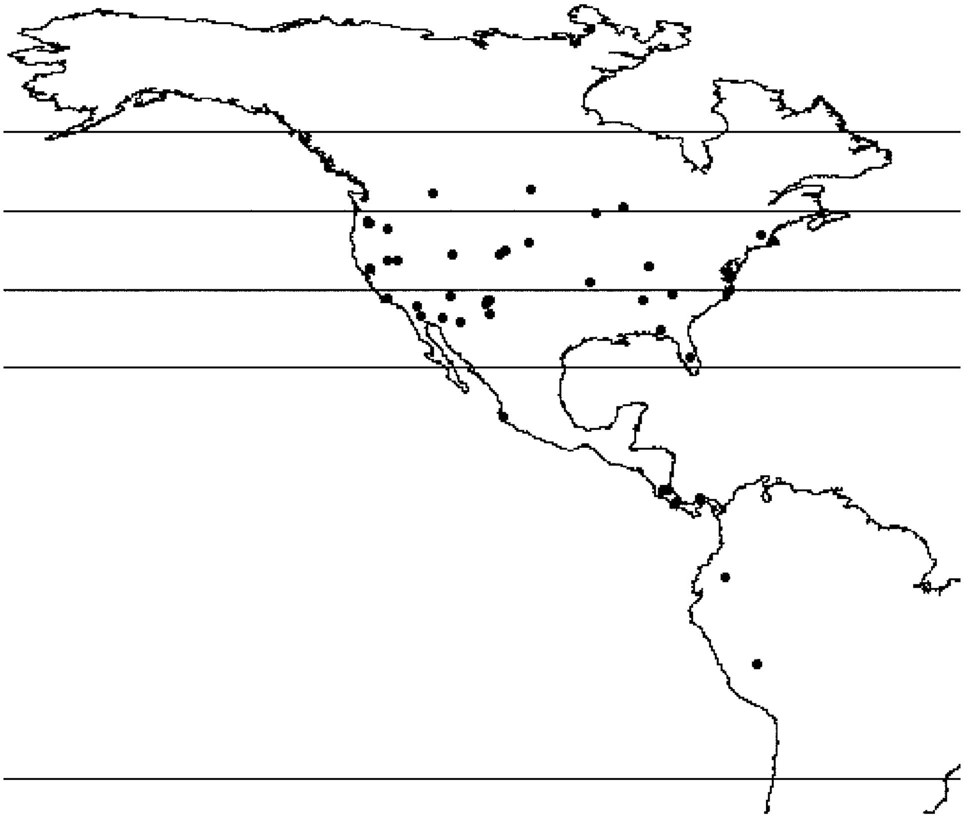

Figure 1: Map of the 49 localities studied; lines delimit four ecoclimate zones of Rosenzweig (1995)

species occupies some fraction of the island (its range) and that any area sampled in that range is equally likely to yield an individual of that species. If so, the size and distribution of species ranges determines the distribution of *S*: *S* anywhere on the island can be determined by counting the number of overlapping species ranges in the sample area (Willig and Lyons 1998; Colwell and Lees 2000). The simplest version of the middomain hypothesis assumes that species ranges are randomly arrayed (Willig and Lyons 1998; Lees et al. 1999). When true, the number of species ranges (and hence *S*) is expected to be low near the barrier, with some maximum near the geometric center of the landmass. This "middomain effect" has been evaluated at grains of 2.5° × 2.5° along New World latitudinal gradients (e.g., pole-equator-pole; Willig and Lyons 1998), 27 × 27-km grains in Madagascar (Lees et al. 1999), and 1° × 1° grains in Africa (Jetz and Rahbek 2001). It provides a simple alternative to other hypotheses for geographical gradients in *S*. Here we test three of its predictions: first, ant diversity shows a parabolic approach to the equator; second, ant diversity is highest in the center of North America; and third, ant diversity is negatively correlated with distance to the nearest ocean.

Area Hypothesis

Gradients in *S* may also arise if more species accumulate where the net balance of speciation to extinction is higher. The area hypothesis (Terborgh 1973; Rosenzweig 1995; Chown and Gaston 2000) arises from two assumptions. First, taxa reach their peak abundance within zones of relatively uniform climate (Kaspari 2001) and are thus limited to latitudinal and elevational bands that produce these "ecoclimate zones" (Merriam 1890, 1898; Rosenzweig 1995; Rosenzweig and Sandlin 1997). The second assumption is that larger ecoclimate zones have a higher net rate of diversification ($P - X$). Larger zones may enhance *P* if they are more easily split by geographic barriers, promoting vicariant speciation (Chown and Gaston 2000); larger zones may decrease *X* if they allow larger species ranges that are less prone to catastrophic extinction (Rosenzweig 1995).

Rosenzweig (1995) proposed four ecoclimate zones (subtropics, temperate, boreal, polar; fig. 1) that fall north and south of the contiguous tropical zone (Terborgh 1973). Our surveys spanned four of these ecoclimate zones in the New World; the tropical zone was three to five times larger than the northern subtropical, temperate, or boreal zones (see "Methods"). We test the assumption that each zone will have a different complement of species and the prediction that S is proportional to the area of the zone (Rosenzweig 1995).

Energy-Speciation Hypothesis

The number of photons striking a unit area of earth increases as one approaches the equator. The energy-speciation hypothesis argues that solar energy limits rates of evolution and, by doing so, limits P (Currie 1991; Rhode 1992; Roy et al. 1998). Rhode (1992) proposed two mechanisms. First, warmer environments may increase mutation rates (Rhode 1992; Roy et al. 1998). Second, warmer environments also tend to be less seasonal. For a given generation time, longer growing seasons may allow for more generations per year (Kaspari et al. 2001) and thus higher rates of sexual recombination. The energy-speciation hypothesis predicts that S should increase with environmental temperature.

The Six Hypotheses and Spatial Grain

We have just reviewed six nonexclusive hypotheses for gradients in S. How do these processes shape diversity at different spatial, temporal, and taxonomic scales (Levin 1992)? Ricklefs (1987) suggested that the hierarchical nature of S (a plot cannot have more species than the plot in which it is embedded) represented a logical starting point; S is ultimately constrained by P. Hypotheses predicting trends in P should thus play a larger role in shaping diversity gradients when comparing plots of larger grain and plots of a fixed grain but at larger spatial extents (e.g., different biogeographic provinces; Cornell 1985; Latham and Ricklefs 1993; Ricklefs and Latham 1993; Ricklefs and Schluter 1993; Qian and Ricklefs 2000). Conversely, processes like migration, extinction, and sampling that act at smaller spatial scales should weaken the speciation signal at smaller grains and extents.

Ricklefs's hierarchy hypothesis has gone largely untested for lack of data on S across multiple spatial scales and for simultaneous tests of hypotheses that variously incorporate P, M, and X (but see Losos and Schluter 2000; Crawley and Harral 2001; Lomolino and Weiser 2001; Lyons and Willig 2002). The six hypotheses above can be roughly ordered on the basis of Ricklefs's hierarchy hypothesis. The sampling hypothesis acts at scales where $N_A \ll S_{A+1}$. For a given S_{A+1}, as plots increase in size and thus accrue more and more individuals, this is less likely to be true (Rosenzweig 1995). The sampling hypothesis should thus be most likely to account for variation at our smallest grain, the 1-m^2 plot (where N rarely exceeds five). As plot size increases, $N_A \gg S_{A+1}$, sampling effects should diminish. The mass-effect hypothesis operates at the landscape scale when adjacent habitats are connected by dispersal. It assumes the plot is small enough to fit within a habitat. If a plot grows too large, it will no longer be subsidized by adjacent habitats; it will contain them. As a plot grows large enough to accrue more and more habitats, the mid-domain effect begins to operate. It assumes that any plot within the geographic range of S species is big enough to include the habitat of each of those species. The abundance-extinction hypothesis can operate at a variety of scales, as long as the array of plots detects variation in taxon abundance large enough to influence local extinction rates. Finally, two hypotheses—the energy-speciation and area hypotheses—assume plots are big enough and far enough apart that they differ markedly in speciation rates. If the Ricklefs hierarchy hypothesis holds, these latter hypotheses should play increasing roles as we scale up.

Methods

We selected 49 localities for this study to maximize coverage of the New World net primary productivity gradient (see appendix in the online edition of the *American Naturalist*; Kaspari et al. 2000*b*). We include four elevational gradients: three in North America (Oregon, New Mexico, and North Carolina) and one in Central America (Costa Rica). Most localities were at biological field stations, nature preserves, or U.S. Long-Term Ecological Research (LTER) sites. All of our temperate sites were in the Northern Hemisphere. Localities were sampled from 1994 to 1997 during seasons of peak ant activity.

At each locality, a transect of 30 1-m^2 plots, separated by 10 m, was laid out randomly with the aid of a topographic map. Ant colonies were counted by first carefully scanning the soil for nests. In localities with leaf litter, each piece of litter (e.g., twigs, rolled leaves, pieces of wood) was inspected for colonies. Plots were then baited with shortbread cookies (Pecan Sandies) and resampled 30 min later. These cookies, with fats, carbohydrates, and proteins, attract all but the most specialized predator ants. Both stray ants from off the plot and those from nests on the plot were recorded. A list of ant species is available from M. Kaspari. Vouchers are in M. Kaspari's collection at the University of Oklahoma.

Each of the 49 sites had a different species inventory of nesting and stray ants. Moreover, we took steps to further minimize spatial autocorrelation in taxonomic composi-

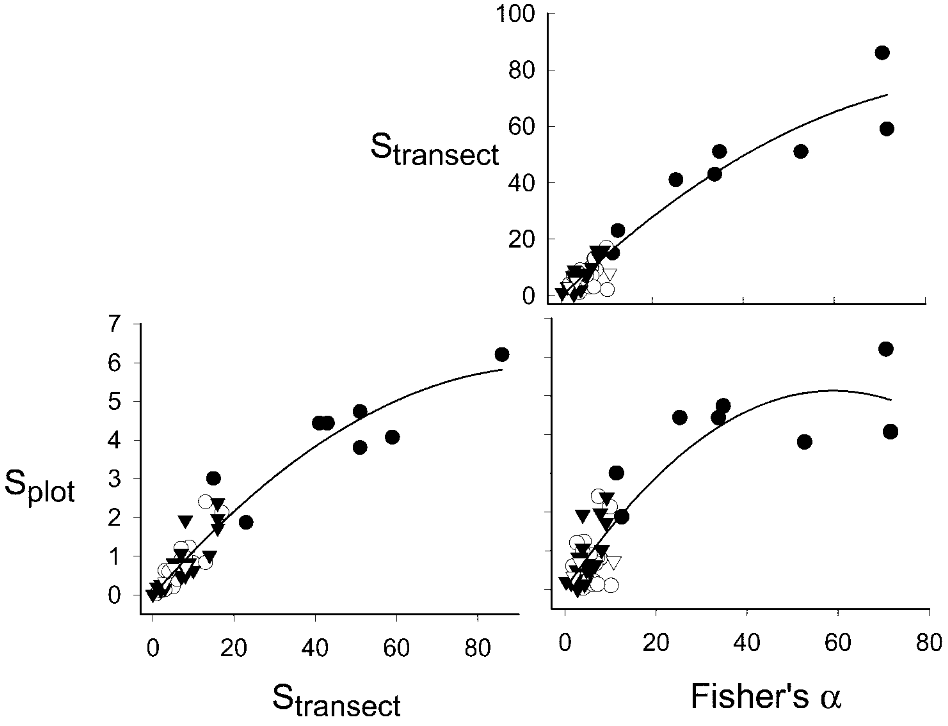

Figure 2: Relationship among the three grains of diversity measured in this study, with the larger grain measure on the *X*-axis. Symbols represent localities from each ecoclimate zone. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal. Lines represent polynomial regressions.

tion (Blackburn and Gaston 1998). First, we identified all sites that shared the same two most abundant nesting species. Eight sites were identified: three eastern forests had *Aphaenogaster rudis* and *Lasius alienus* as dominants, two east central forests had *A. rudis* and *Paratrechina faisonensis*, and three northwest forests had *Lasius pallitarsis* and *Leptothorax muscorum*). For each set, we randomly eliminated all but one site, leaving 44 localities for our most intensive analysis.

Species Richness

We quantify diversity in the ants that nest and forage on the ground. In practice, this means that we likely undersample subterranean species and ignore those that nest in the forest canopy. The canopy ant fauna increases in richness from subtropical to tropical forests, where it may reach rough parity with the ground fauna (see fig. 3 of Longino and Colwell 1997). Assuming no overlap in species composition between canopy and soil fauna (Yanoviak and Kaspari 2000), this suggests that our estimates of total tropical ant diversity would be two times higher than we report. However, as diversity varied 300 times across our study sites, this bias is unlikely to affect our conclusions.

We measured S at three spatial grains. First, we counted the number of species nesting in an average 1-m^2 plot over the course of a 1-wk survey (S_{plot}). Next, we counted the number of species nesting on a transect of 30 1-m^2 plots, each plot separated by 10 m (S_{transect}). Both of these measures are absolute counts (as opposed to estimates) of S, since in the approximately 20–360 min we spent at each plot, it is unlikely we missed a species. Such a measure is often referred to as species density (e.g., Gotelli and Colwell 2001); S_{plot} and S_{transect} represent an order of magnitude increase in area.

We measured diversity at our largest grain by viewing the 1-m^2 plots arrayed across each of our sites as subsamples of ant diversity at a larger, but unspecified, local scale. A variety of methods use subsamples to generate an estimate of species richness (e.g., jackknife 2; Colwell and Coddington 1994). We used Fisher's α, a scalar that integrates the effects of P and N and removes the sampling effect (Fisher et al. 1943; Rosenzweig 1995; Hubbell 2001). We calculated Fisher's α with EstimateS (Colwell 1997) after tallying the number of plots in which each species, nest and stray, was recorded. As it removes the competing sampling hypothesis, Fisher's α is particularly useful for detecting the signature of the abundance-extinction hy-

Table 1: Polynomial regression of the effect of large-scale diversity measures on small-scale diversity measures

Variable	Estimate	$pr > \|t\|$
S_{plot}:		
Intercept ($F = 216.01$, $r^2 = 0.91$)	−.03542	.7637
Transect	.11934	<.0001
Transect^2	−.00059	.0009
Intercept ($F = 82.53$, $r^2 = 0.80$)	−.04988	.7824
Fisher's α	.17564	<.0001
Fisher's α^2	−.00149	.0002
$S_{transect}$:		
Intercept ($F = 243.16$, $r^2 = 0.92$)	−.4167	.7594
Fisher's α	1.5661	<.0001
Fisher's α^2	−.0079	.0053

Note: In all but one case, there is a positive decelerating relationship.

pothesis. Moreover, other measures of diversity that remove sampling effects (e.g., jackknife 2) provide qualitatively identical results in our analyses.

To test the sampling and abundance-extinction hypotheses, we measured N as the total number of ant colonies recorded on a transect. A single ant colony may occupy more than one litter nest (Herbers 1985) or have more than one nest opening in the soil (Davidson et al. 1985). Both behaviors make this method of estimating abundance less precise. However, if we use a more conservative method of estimating abundance—counting each species in a 1-m^2 plot no more than once—our conclusions are not changed.

To further evaluate the sampling hypothesis, we constructed a null expectation for S_{plot}. The null assumes that the number of ant species nesting in each of a locality's 30 1-m^2 plots was sampled randomly from the species-abundance distribution generated by $S_{transect}$ (Gotelli and Entsminger 2001). For example, at a locality, 20 plots yield two colonies and 10 plots yield three colonies. The null expectation was calculated from the mean of 20 samples (with replacement) of two colonies from $S_{transect}$'s species abundance distribution and 10 samples of three colonies. The mean of 500 of these randomizations was calculated for each of the 44 localities and used to generate the null curve for S_{plot} versus N. The null and observed curves were compared with ANCOVAs.

To test the mass-effect hypothesis, the elevational range of a site was measured within 10- and 100-km-radius circles using level measures from the Digital Terrain Elevation Database from the U.S. National Imagery and Mapping Agency. They performed similarly, and only the 10-km radius is included in the analysis presented here.

To test the middomain effect, the latitude and longitude of each site was measured, and the distance from the nearest ocean was calculated with ArcINFO GIS.

To test the area hypothesis, the area of our four New World ecoclimate zones (Rosenzweig 1995)—the tropics (26°S–26°N latitude, 1.58×10^{13} m^2), subtropical zone (26°–36°N, 3.18×10^{12} m^2), temperate zone (36°–46°N, 4.81×10^{12} m^2), and boreal zone (46°–56°N, 4.93E+12 m^2)—was calculated with ArcINFO GIS.

To test the energy-speciation hypothesis, mean monthly temperatures were calculated from on-site records or nearby airports. Potential evapotranspiration, often used as a proxy of solar energy (e.g., Currie 1991), gave the same results as temperature in our analyses.

Statistics

We $\log_{10}$ transformed the data both to improve normality and to more evenly weight the distribution of diversity values, since the eight tropical sites reflect up to 75% of the range of observed S. To $\log_{10}$ transform the temperature data, 3° were added to all 49 sites to account for our tundra site's value of −2.3°C.

We first evaluated the six hypotheses separately. We tested for the sign of the relationship between S and the independent variable with Spearman rank correlations. Next, we used linear regression to extract a scaling exponent (e.g., $Y = cX^{\exp}$) and an estimate of the variance explained (r^2). As the relationship sometimes appeared to be triangular, which suggests a constraint function (Brown

Table 2: Diversity of three localities in eastern North America infested and uninfested by the imported fire ant *Solenopsis invicta*

Locality	Latitude	$S_{transect}$	Fisher's α
Uninfested:			
Myles Standish SP, Massachusetts	42.0	16	9
Harvard Forest LTER, Massachusetts	42.5	7	3.9
Virginia Coast LTER, Virginia	37.3	16	9.2
Average		13	7.4
Infested:			
Bankhead NF, Alabama	34.4	13	7.3
Torreya SP, Florida	30.6	17	9.9
Ordway Prairie, Florida	27.2	9	7.7
Average		13	8.3

Note: SP = state park, LTER = National Science Foundation Long-Term Ecological Research site, NF = national forest.

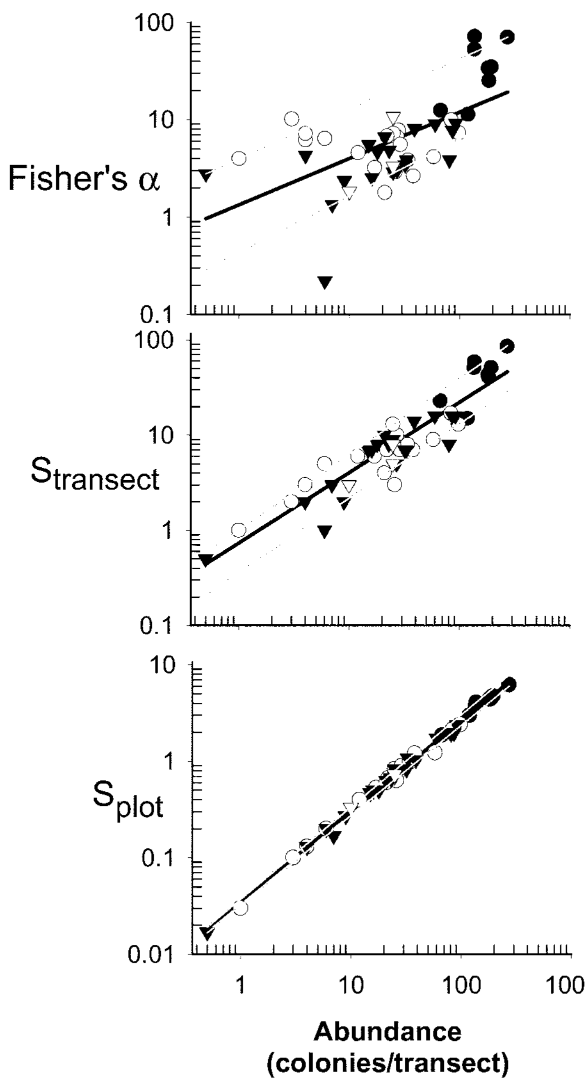

Figure 3: Tests of the sampling and abundance-extinction hypotheses, which predict positive decelerating diversity-abundance curves. Black lines are the least square means linear regression; gray lines are least absolute deviation regressions through the ninetieth and tenth quantile. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal.

1995; Blackburn and Gaston 1998; Kaspari et al. 2001), we next used least absolute deviation regression to describe the upper ninetieth and lower tenth quantiles (Slauson et al. 1994; Mielke 1998; Scharf et al. 1998). Finally, we used stepwise multiple regression (Draper and Smith 1981) to evaluate the relative ability of the six hypotheses to account for the variation in S. We set $p < .05$ as the criterion for a variable to enter and remain in the model.

We reran our stepwise regressions twice to examine two scenarios. First, since we had dropped five localities to decrease redundancy in species composition, we reran the regressions for the complete 49-site data set. Second, in order to better compare our results with those from other North American diversity studies (e.g., Currie 1991), we analyzed the North American sites alone.

Results

We collected >5,000 species records and 721 ant species from the 44 localities (see appendix in the online edition of the *American Naturalist*). Most species could be identified with existing keys and collections; 303 (42%) have yet to be formally described.

Diversity varied from desert to rain forest (fig. 2); S_{plot} ranged from 0 nesting species m^{-2} in a midelevation Oregon forest (with seven species wandering through its plots) to an average of 6.2 species m^{-2} in a lowland Ecuador rain forest; S_{transect} varied from 0 to 86 species for the same two localities. Fisher's α (which generates an estimated diversity from both nest and stray records) varied 325-fold, from 0.22 in alpine tundra to 71.6 in a Peruvian low-elevation rain forest. The tropics at each grain accounted for ~75% of the variation in diversity. For example, S_{transect} varied from 0 to 17 nesting species 30 m^{-2} in the temperate zone but from 15 to 86 nesting species 30 m^{-2} in the tropics, with low values for the Costa Rican cloud forest and Mexican dry forest and the highest values for the two Amazonian lowland wet forests.

The three diversity measures were correlated (r_s = 0.65–0.94, $n = 44$, $p < .0001$). Polynomial regressions of small-scale versus large-scale measures showed positive decelerating curves (fig. 2; table 1); S, particularly at the m^2 scale, increased at a slower rate as more species were added to the species pool. Individual plots thus represented a smaller fraction of the locality's diversity at more diverse sites.

Numerous studies have shown that two invasive ant species, the argentine ant (*Linepithema humilis*; Ward 1987; Human and Gordon 1997; Holway 1998) and the red imported fire ant (*Solenopsis invicta*; Porter 1988; Gotelli and Arnett 2000; Kaspari 2000), can significantly decrease biodiversity. Our localities were embedded in regions infested with *L. humilis* (two localities) and *S. invicta* (three localities). Only one of each recorded an invasive ant, and all maintained a species complement apparently normal for the area (M. Kaspari, personal observation). Contrary to Gotelli and Arnett (2000), diversity did not appear to peak just above *S. invicta*'s northern range limit (table 2) but was relatively invariant with latitude.

Table 3: Analysis of five independent variables key to the six hypotheses tested in this study

	Linear regression								Quantile regression		
Measure	F	r^2	c	p	exp	p	$F_{\mathrm{exp}=1}$	p	Quantile	exp	p
S_{plot}:											
Abundance	7619	.99	.04	<.0001	.933	<.0001	39.2	<.0001	.9	.956	.0002
			.02		.01				.1	.934	.0002
Elevation range	4.59	.10	5.36	.0854	−.336	.0379	72.6	<.0001	.9	−.080	.35
			.41		.16				.1	−.419	.047
Distance to ocean	2.77	.06	1.88	.3029	−.167	.1036	135.6	<.0001	.9	−.240	.0334
			.26		.10				.1	.175	.5394
Temperature	5.23	.11	.12	.012	.672	.0273	1.2	.271	.9	.817	.0002
			.35		.29				.1	−.110	.66
Area	24.2	.37	.00	<.0001	1.353	<.0001	1.6	.2068	.9	.978	.0002
			3.50		.28				.1	1.875	.006
S_{transect}:											
Abundance	231.1	.85	.74	.0777	.739	<.0001	28.9	<.0001	.9	.797	.001
			.07		.05				.1	.780	.0002
Elevation range	4.3	.09	42.24	<.0001	−.279	.0447	89.8	<.0001	.9	−.144	.97
			.36		.14				.1	−.532	.055
Distance to ocean	3.9	.08	20.82	<.0001	−.167	.0554	188.8	<.0001	.9	−.317	.0458
			.22		.08				.1	−.139	.8708
Temperature	15.0	.26	.72	.6126	.890	.0004	.2	.6333	.9	1.025	.0002
			.28		.23				.1	.299	.904
Area	33.9	.45	.00	<.0001	1.284	<.0001	1.7	.2055	.9	1.095	.0002
			2.80		.22				.1	1.687	.06
Fisher's α:											
Abundance	25.5	.38	1.34	.3848	.476	<.0001	30.8	<.0001	.9	.513	.0002
			.14		.09				.1	.586	.001
Elevation range	1.1	.03	14.41	.0023	−.141	.3034	71.3	<.0001	.9	−.025	.995
			.36		.14				.1	−.019	.96
Distance to ocean	7.4	.15	21.29	<.0001	−.215	.0096	235.9	<.0001	.9	−.359	.083
			.21		.08				.1	−.234	.069
Temperature	51.6	.55	.22	.0028	1.243	<.0001	2.0	.1683	.9	1.328	.0006
			.21		.17				.1	.825	.0002
Area	27.5	.40	.00	<.0001	1.167	<.0001	.6	.4577	.9	1.410	.002
			2.83		.22				.1	1.257	.09

Note: Least squares linear regression and quantile regression are used to determine the relationship between each $\log_{10}$-transformed variable and $\log_{10}$ diversity (i.e., $Y = cX^{\mathrm{exp}}$). For linear regression, standard deviations are provided below c and exponent.

Individual Tests of the Six Hypotheses

Abundance (N; the number of ant colonies present on a transect of 30-m^2 plots in 1 wk of sampling) varied from 0 colonies in an Oregon fir forest to 272 colonies in an Ecuadorian lowland rain forest (fig. 3); N was correlated with S_{plot} ($r_s = 0.99$), S_{transect} ($r_s = 0.89$), and Fisher's α ($r_s = 0.64$; $n = 44$, $p < .0001$ for all correlations). Linear regressions of log S on log N yielded significant and positive decelerating curves (i.e., power functions with exponents <1.0; table 3). The exponent of these curves began near unity (0.93) for S_{plot} and fell to 0.74 for S_{transect} and down to about 0.48 for Fisher's α. Quantile regressions were all highly significant ($p < .0002$; table 3), with the exponents for the ninetieth and tenth quantiles varying by <0.10.

The distribution of localities around the linear regression line became more complex beyond S_{plot}. The alpine tundra assemblage (six colonies of *Formica neorufibarbis*) increasingly anchored the scatterplot. Furthermore, the species-poor warm deserts and species-rich tropical forests diverged upward from each regression line (e.g., when the eight tropical forests were removed, regression exponents decreased by 0.11 for S_{transect} and 0.30 for Fisher's α).

Sampling Hypothesis. The sampling hypothesis predicts positive, decelerating relationships between abundance and diversity. It assumes that species in a plot are a random sample of those available in the source pool. We can evaluate this assumption for S_{plot} given our estimate of the species pool at the next highest S_{transect} scale. Our null model

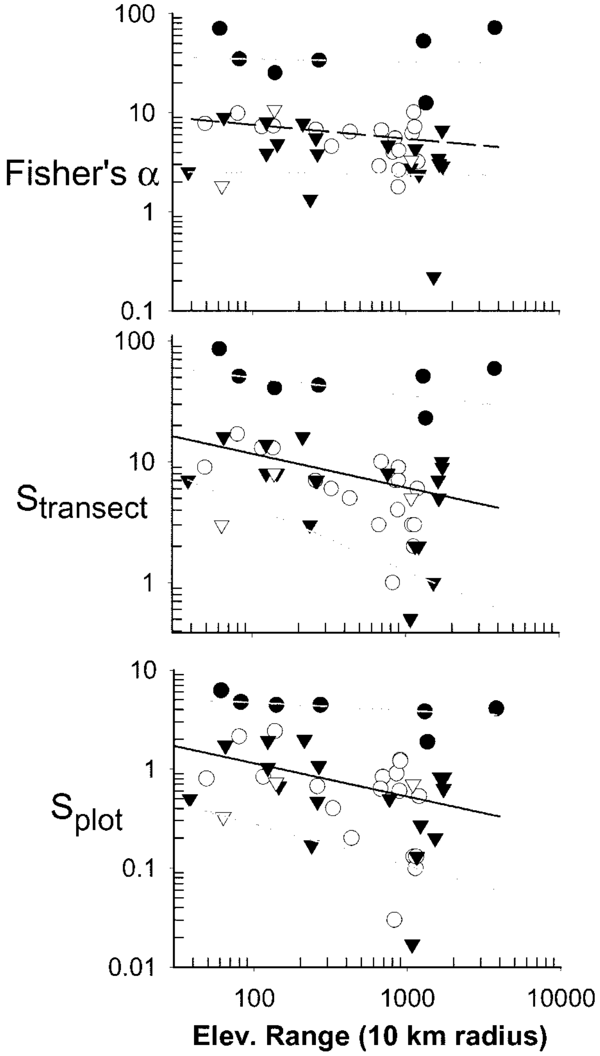

Figure 4: Test of the mass-effect hypothesis, which predicts higher diversity as elevational range increases. Elevational range is maximum–minimum elevation within a 10-km radius of the locality. Black lines are the least square means linear regression; gray lines are least absolute deviation regressions through the ninetieth and tenth quantile. Dashed lines are not significant at $p < .05$. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal.

generated an S_{plot} that scaled as $N^{0.95}$, close to the observed exponent of 0.93. These exponents did not differ (H: null = observed exponents; ANCOVA, $F = 2.64$, df = 1, 86, $p = .108$).

Abundance-Extinction Hypothesis. The abundance-extinction hypothesis also predicts positive, decelerating relationships between abundance and diversity, but at larger spatial scales. Fisher's α, designed to remove the sampling effect, retained a positive, decelerating abundance-diversity curve close to 0.48 (table 3).

Mass-Effect Hypothesis. The 44 localities used here were embedded in landscapes that varied two orders of magnitude in their elevational range: from 38 m within a 10-km radius in a Minnesota savanna to >3,000 m in the Peruvian Andes. The mass-effect hypothesis posits that squeezing more elevational range into a given area will enhance a locality's species richness by increasing immigration from disparate habitats.

Species richness (S) did not increase and twice marginally decreased with elevational range for S_{plot} ($r_s = -0.27$, $p = .073$) and $S_{transect}$ ($r_s = -0.27$, $p = .061$; fig. 4). Fisher's α behaved similarly ($r_s = -0.20$, $p = .186$). Linear regressions of log S on log-elevational range yielded exponents that indicated negative deceleration for S_{plot} (-0.33) and $S_{transect}$ (-0.28; p's $< .05$) but with considerable scatter ($r^2 < 0.10$; table 3). Quantile regressions suggest that this negative relationship was largely due to the tenth quantile, which had exponents 0.40 lower than did the ninetieth. At the largest grain, Fisher's α, both linear and quantile regressions failed to find significant relationships with elevational range.

Middomain Hypothesis. Latitude ranged from 48.4° for a North Dakota prairie to 0.6° for an Ecuadorian lowland forest (we use the absolute value of latitude for a Peruvian lowland forest at −11.8°, our one Southern Hemisphere locality); S_{plot} and $S_{transect}$ decreased with latitude ($r_s = -0.46$ and -0.61, $p < .0001$); Fisher's α behaved similarly ($r_s = -0.64$, $p < .0001$). In all cases, this appeared to be driven primarily by the tropical localities; S showed no clear trend with latitude in North America. For example, our highest-latitude North Dakota prairie site yielded the third highest Fisher's α in North America (fig. 5).

We tested three predictions of the middomain hypothesis (fig. 5). First, we tested for a parabolic diversity curve as one travels from the boreal zone toward the equator. Quadratic regression, in contrast, suggested a diversity curve that was concave up, not concave down (fig. 5), and that accounted for 77%–87% of the variation (table 4). We next tested for a unimodal (i.e., hump-shaped) diversity curve in a longitudinal sample across North America. Longitude ranged from −70.7° for a Massachusetts woodland to −122.3° for a California coastal woodland. Both S_{plot} ($r_s = 0.65$) and $S_{transect}$ ($r_s = 0.47$; p's < -0.004) increased from west to east; Fisher's α failed to vary with longitude ($r_s < 0.22$, $p > .05$). Polynomial regression suggested that S_{plot} and $S_{transect}$ showed a weakly negative and decelerating relationship from east to west (table 4; fig. 5). This pattern was more strongly expressed for S_{plot} ($r^2 = 0.44$) than for $S_{transect}$ ($r^2 = 0.15$) and not at all for Fisher's

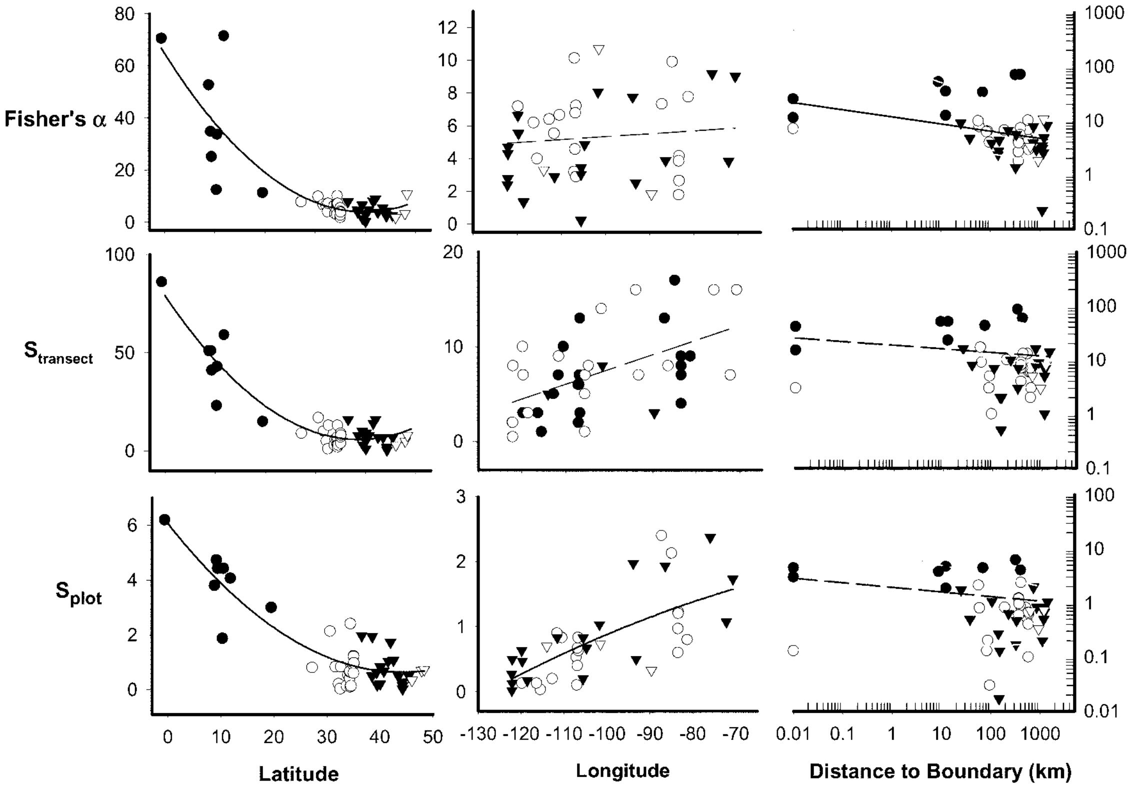

Figure 5: Testing three predictions of the middomain hypothesis. Diversity is predicted to show a parabolic increase toward the equator (*left column*), show a hump-shaped relationship across North America (*middle column*), and increase with distance from the ocean (*right column*). Black lines are the least square means linear regression; gray lines are least absolute deviation regressions through the ninetieth and tenth quantile. Dashed lines are not significant at $p < .05$. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal.

α. Our third test of the middomain hypothesis evaluated the prediction that S should decrease as one approaches an ocean barrier. Minimum distance to the ocean varied from 0 km (for a Massachusetts woodland and Mexican dry forest) to 1,419 km for a Nebraska grassland (fig. 5). Contrary to prediction, S either failed to vary (S_{plot}: $r_s = -0.19, p = .21$; S_{transect}: $r_s = -0.26, p = .08$) or decreased as a locality grew farther from the ocean (Fisher's α: $r_s = -0.39$, $p = .01$). This decrease was a shallow (exponent approximately −0.10) negatively decelerating curve that accounted for 13% of the variance in Fisher's α (fig. 3).

Area Hypothesis. Our surveys spanned four of Rosenzweig's (1995) New World ecoclimate zones: the tropical zone was three to five times larger than the north subtropical, temperate, or boreal zones (fig. 6). We tested two elements of the area hypothesis: that species are restricted to ecoclimate zones and that larger ecoclimate zones yield proportionately higher S. First, of the 486 tropical species, only two (<1%) were collected in the three temperate zones. Endemism, however, breaks down as one leaves the tropics. The subtropics shared 52% and 12% of its species with the temperate and boreal zones, the temperate zone shared 42% and 26% of its species with the subtropical and boreal zones, and the boreal zone shared 74% and 34% of its species with the temperate and subtropical zones.

The area-speciation hypothesis also predicts that a sample from the tropics should be three to five times more diverse than a sample from one of the three temperate zones; S was correlated with area for S_{plot} and S_{transect} ($r_s = 0.48$, $p < .0011$; fig. 6) and less well correlated for Fisher's α ($r_s = 0.33, p = .0285$). There is little difference in S among the boreal, temperate, and subtropical zones (despite the smaller size of the latter). However, the tropics are eight times more diverse than the three temperate zones (see also fig. 5). In a linear regression, log area accounts for about 40% of the variation in log S across all three measures (table 3). Despite exponents as high as 1.35 for S_{plot}, F-tests fail to find significant deviations from unity (p's > .20). Quantile regressions yielded two pat-

Table 4: Stepwise polynomial regressions of diversity on latitude and longitude (North American localities only)

	Latitude ($n = 44$)					Longitude ($n = 36$)				
Measure	F	r^2	Intercept	Latitude	Latitude^2	F	r^2	Intercept	Longitude	Longitude^2
S_{plot}	82.2	.80	6.3***	−.27***	.003***	26.2	.44	2.3***	…	−.00014***
S_{transect}	140.5	.87	79.1***	−3.79***	.049***	10.8	.24	16.3***	…	−.00075**
Fisher's α	66.8	.77	66.3***	−3.16***	.040***	…	…	…	…	…

** $p < .01$.

*** $p < .001$.

terns: S_{plot} had significant tenth and ninetieth quantiles ($p < .008$); S_{transect} and Fisher's α had nonsignificant tenth quantiles ($p > .05$) and highly significant ninetieth quantiles ($p < .002$).

Energy-Speciation Hypothesis. Mean monthly temperature varied by an order of magnitude in this study, from −2.5°C for Colorado alpine tundra to 27.3°C in the Peruvian lowland rain forest. The energy-speciation hypothesis predicts a positive correlation between a locality's temperature and S; S was correlated with mean monthly temperature for S_{plot} ($r_s = 0.42$, $p = .004$) and S_{transect} ($r_s = 0.51$, $p = .0004$); correlations were higher for Fisher's α ($r_s = 0.67$, $p < .0001$) since these scatterplots were increasingly anchored by the one-species tundra assemblage (fig. 7). Linear regressions yielded exponents of log temperature on log S that increased from S_{plot} (0.67) to S_{transect} (0.89) to Fisher's α (1.24) with a similar increase in r^2s (0.11, 0.26, 0.55). Quantile regressions yielded positive exponents for the ninetieth quantile (0.82, 1.00, 1.33), but a tenth quantile that was initially flat rotated upward at higher grains (−0.11, 0.30, 0.83). While cold localities typically had few species, warm localities could be species-poor deserts or species-rich tropical rain forests.

Synthesis of Models across Scales

The six hypotheses accounted for different portions of variance depending on the grain of analysis (table 5). However, elevational range (the mass-effect hypothesis) and distance to the ocean (the middomain hypothesis) never entered the stepwise regressions, although they accounted for a maximum of 10% and 15% of the variation for at least one spatial grain.

At the smallest grain, S_{plot}, abundance accounted for 99.5% of the variance in species richness across the 44 sites. No other variable entered the regression model. Combined with the close match to the expected N-S_{plot} curve, this suggests that the ant diversity gradient at the 1-m^2 plot scale is driven largely by sampling.

At the intermediate grain, S_{transect}, abundance accounted for 85% of the variation in species richness (table 5). Moreover, two additional variables, mean monthly temperature and the ecoclimate zone area (uncorrelated in this study; $r_s = 0.016$, $p > .90$), account for an additional 6% of the variation.

At the largest but spatially ambiguous grain of Fisher's α, mean monthly temperature (55%) and the ecoclimate zone area (20%) account for three-fourths of the variation in diversity. Abundance, in contrast, accounts for only 2% of the variation.

We reran stepwise regressions for both the total data set of 49 sites and for North America alone (table 5). Including the dropped five localities failed to qualitatively change our results with one exception: the loss of abundance as a significant effect in the Fisher's α regression. When only North American sites are analyzed, the effect of ecoclimate zone area disappears.

Discussion

Diversity gradients arise from a hierarchy of process: speciation forms new species; species populations colonize habitats and expand their ranges; local populations drift and are driven to extinction. Furthermore, the sampling protocols that record these processes capture different numbers of individuals. Four hypotheses that variously incorporate speciation, immigration, extinction, and sampling account for between 75% and 99% of the observed variation in local ant diversity at geographic extents. The relative weight of their contribution varies with spatial grain. For example, our results suggest that one must focus on factors that enhance colony abundance (these include high plant productivity, warm summers, and cold winters; Kaspari et al. 2000*b*) to understand patterns of ant species richness at 1-m^2 scales. To understand gradients of S beyond the transect scale, one must focus on factors like ecoclimate area and temperature that are linked to the balance of speciation to extinction (Labandeira and Sepkoski 1993; Rosenzweig 1995; Roy et al. 1998; Cardillo 1999). Even at the transect scale and consistent with Ricklefs's (1987) hierarchical theory of biodiversity, factors linked to speciation and extinction leave a small but clear signal.

Measuring diversity at multiple scales is an important step toward the development of diversity theory. Studies of sessile organisms are useful means to this end, since abundance and species richness can both be measured relatively unambiguously (Hubbell 1979; Collins and Glenn 1990). This study identifies diversity at three grains. Two, S_{plot} and S_{transect}, are absolute counts of all the species nesting in those plots. Our third grain, Fisher's α, calculated from the nests and strays collected on the 330-m transect, corresponds to another way of measuring diversity (and what some ecologists appear to mean when they use the word "local"): an estimate of total species diversity from subsamples confined to a relatively small area. While estimating diversity through subsamples is often a practical necessity (e.g., on a 50-ha plot in Panama, one can reliably record every tree >1 cm dbh [Condit 1995] but not every herbivorous beetle >1 mm in length [Erwin 1986]), they do so at a cost: the ability to precisely define the spatial grain of the measurement. This can lead to problems of interpretation.

For example, one way of exploring how the processes limiting S vary with spatial scale is to examine the curves that result when S at grain A is plotted against grain $A + 1$ (Cornell 1985; Cornell and Lawton 1992). These two grains have often corresponded to estimates of "local" and "regional" species richness. A decelerating curve implicates processes that limit local diversity, with complete saturation suggesting the predominance of local process (Cornell 1985; Cornell and Lawton 1992). A linear curve, in contrast, suggests that local diversity mirrors (or samples) regional diversity and is thus limited by processes acting at that larger scale (but see Rosenzweig and Ziv 1999). Such interpretations, however, are sensitive to how data are collected. If a protocol of subsampling + diversity estimation is used to measure S_A, this leads to problems that directly result from S_A's spatial ambiguity. For example, some authors (Caley and Schluter 1997; Karlson 2002) warn of "pseudosaturation," decelerating curves of S_A versus S_{A+1} that result when the small plots are too small to capture the diversity they are meant to estimate. Absolute species counts avoid this problem. Here we show that along the terrestrial productivity gradient, ant communities yield decelerating curves of S_A versus S_{A+1} (fig. 2). Beyond an α of 20 and S_{plot} of five, it is difficult to squeeze any more ant species into a m^2 quadrat. Note this is not an "artifact" of sampling. It is a real phenomenon that reflects how productivity and body size, which determine how individuals are packed into their environment, combine to constrain diversity (Brown 1981; Kaspari et al. 2000*b*; Enquist and Niklas 2001).

The species richness of these 1-m^2 plots scales almost uniformly to ant abundance ($S \sim N_{\mathrm{plot}}^{0.93}$), which varies 200-fold from desert to rain forest (Kaspari et al. 2000*b*). Gradients of diversity, even at these tiny scales, have implications for the grain of species interactions. A small herb that depends on local colonies for defense against herbivores (Tilman 1978; Cushman and Addicott 1989) or for seed dispersal (Beattie 1985; Levey and Byrne 1993) may have 200-fold more species to deal with (i.e., 200 times the number of potential species interactions) in a tropical forest than in a warm desert.

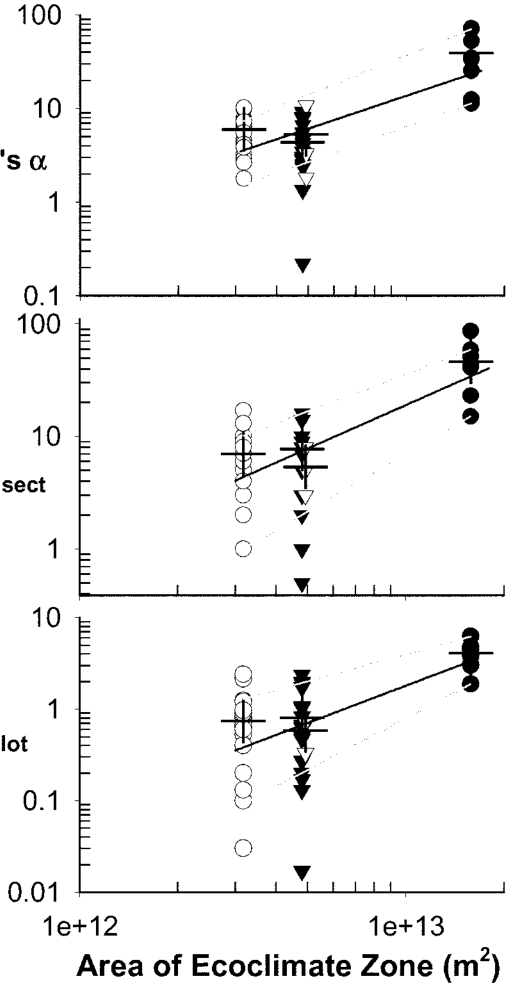

Figure 6: Test of the area hypothesis, which predicts diversity should be proportional to the area of the ecoclimate zone. Black lines are the least square means linear regression; gray lines are least absolute deviation regressions through the ninetieth and tenth quantile. Dashed lines are not significant at $p < .05$. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal; *plus sign*, means for each zone.

Our largest spatial grain, Fisher's α, scales weakly with abundance (table 5). As Fisher's α eliminates the sampling effect, this result supports the hypothesis that high abundance lowers extinction rates. N-S curves can tell us more. For example, S increases less rapidly than N at all three grains: from $N^{0.93}$ for S_{plot} to $N^{0.50}$ for Fisher's α. These

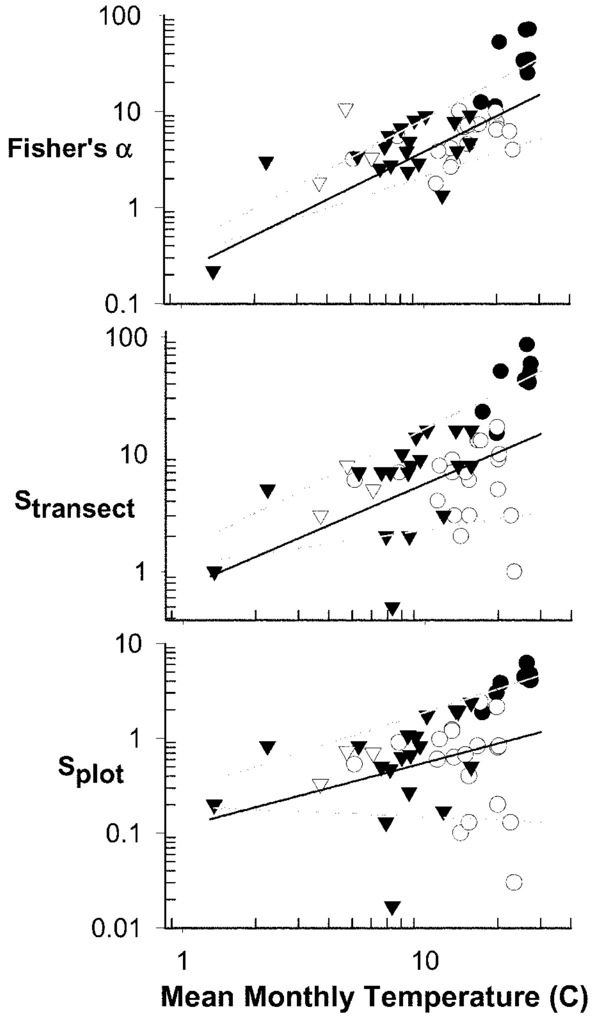

Figure 7: Test of the energy-speciation hypothesis, which predicts a positive relationship between mean monthly temperature and diversity. Black lines are the least square means linear regression; gray lines are least absolute deviation regressions through the ninetieth and tenth quantile. Dashed lines are not significant at $p < .05$. Ecoclimate zone: *solid circle*, tropical; *open circle*, subtropical; *solid triangle*, temperate; *open triangle*, boreal; *plus sign*, means for each zone.

curves thus suggest that the average densities of ant species populations in the highest-diversity area are higher than those in low-diversity areas. Moreover, deserts and rain forests at either end of the abundance gradient fall above the scaling line (fig. 3), suggesting that these biomes have relatively more species per unit abundance. In other words, desert and rain forest habitats maintain their ant species at lower densities than other biomes. We are unaware of any other study that has shown this pattern (biogeographic data sets on N and S are rare). If true, desert and rain forest species may have traits, such as decreased niche overlap or enhanced dispersal ability, that better allow them to increase when rare (MacArthur 1972; Tilman 1997; Rosenzweig and Ziv 1999; Hubbell 2001). The opportunity for such traits to evolve would be enhanced if these biomes were less likely to disappear during recent glaciation events or if their populations have faster evolutionary clocks, as Rhode (1992) proposes.

The mass-effect hypothesis builds M into gradients of diversity. However, contrary to the mass-effect hypothesis, elevational range is negatively correlated with a locality's diversity and never accounts for variation when competing with the five other hypotheses. Our results contrast with studies of North American vertebrates (Kerr and Packer 1997) and butterflies (Kerr et al. 1998) that find increases in diversity with elevational range at the larger grains of 2° × 2° or more. We suggest that spatial grain underlies the differences in our results. At grains the size of latitude-longitude blocks, a plot that includes a mountain will sum over many biomes (i.e., in central Utah, a 2° × 2° block will include tundra and desert shrubland). A plot with a mountain should thus tally more species than a matched plot on a flatter landscape. However, mountainsides also squeeze biomes together, decreasing the area allotted to each (e.g., a strip of ponderosa pine forest on a mountainside will have fewer trees than a similar forest on broad mesa). If extinction rate increases as biome area decreases and species are specialized to biomes, then a 330-m transect embedded on a mountainside should sample fewer species than a matched transect on a flatter landscape. How the effects of dispersal, extinction, and sampling vary with grain size in studies of elevational gradients of diversity is developed further in a companion article (M. Kaspari, unpublished manuscript).

The middomain hypothesis states that the properties of species ranges bounded by barriers produce nonlinear gradients of S. Three predictions of the middomain hypothesis were not supported in this study. First, local ant diversity did not decelerate as one approached the tropics; it accelerated. Second, it was not a unimodal function of longitude across North America; it tended to decrease from east to west. Third, it did not increase as one moves farther from the oceans; it decreased. Nonetheless, the middomain effect has been implicated in studies of diversity for a variety of taxa across Madagascar (grain = 27 × 27 km; Lees et al. 1999) and central Africa (grain = 1° × 1°; Jetz and Rahbek 2001). Again, we suggest that the spatial grain of analysis may explain our divergent results. As grain decreases, a key assumption of the middomain hypothesis—that diversity can be tallied by the overlap of species ranges—is increasingly violated. Species range maps are fractal surfaces that represent patches of individuals, not uniform sheets of equal density (Whittaker 1952, 1956; Brown 1995). Local studies like ours are more likely to

Table 5: Results of stepwise regression on ant diversity at four scales for three versions of the data set

	Minimizing taxonomic overlap ($n = 44$)			Maximizing sample size ($n = 49$)			North America only ($n = 41$)		
Variable	exp	Partial r^2	p	exp	Partial r^2	p	exp	Partial r^2	p
S_{plot}:									
Abundance	.93	.995	.0001	.93	.995	.0001	.93	.992	.0001
Total r^2		.995			.995			.992	
S_{transect}:									
Abundance	.60	.85	.0001	.60	.84	.0001	.60	.79	.0001
Temperature	.37	.05	.0002	.38	.05	.0001	.31	.06	.0007
Area	.31	.02	.0124	.32	.02	.0040			
Total r^2		.91			.91			.85	
Fisher's α:									
Temperature	.97	.55	.0001	.89	.54	.0001	.82	.51	.0001
Area	.66	.20	.0005	1.01	.21	.0001			
Abundance	.16	.02	.0424						
Total r^2		.77			.75			.51	

Note: Abundance, mean monthly temperature, and the area of the ecoclimate zone account for different amounts of variance with spatial grain.

pick up this variation, sampling some habitats and not others, and thus violate the hypothesis's assumption of uniform detectability.

The Coaction of Temperature and Area

The contribution of both temperature and area to gradients of S_{transect} and Fisher's α argues against a single mechanism for latitudinal gradients of diversity; either alone cannot account for figure 2's acceleration of ant diversity toward the tropics (see also Kerr et al. 1998). Analyzed separately, both suggest linear relationships with exponents not significantly different from 1 (table 3).

The area of a locality's ecoclimate zone accounts for about one-fifth of the observed variation in Fisher's α. However, we are circumspect about accepting the area hypothesis as currently outlined (Rosenzweig and Sandlin 1997). First, our result arises statistically because a site in the tropical zone had roughly eight times more species than one in North America. An analysis of diversity gradients in North America alone yields no significant variation accounted for by the ecoclimate zone area (table 5); instead, our results concur with those of Currie (1991) and Kerr and Packer (1997) that show positive, decelerating effects of energy availability on vertebrate diversity. Second, the area hypotheses' assumption of endemism in each zone is clearly violated within North America: the subtropics, temperate, and boreal zones share between 12% and 74% of their species. Perhaps what constitutes an ecoclimate zone requires fine-tuning so as to better meet the endemism assumption (e.g., the wet subtropics of southeastern North America share few species with the desert subtropics of the American Southwest; Creighton 1950).

In the end, the best test of the area hypothesis may be its ability to make sense of between-region patterns of diversity. Although standardized surveys of ant diversity (e.g., Agosti et al. 2000) are rare, some data are consistent with the area hypothesis. For example, Australia's tropical zone is about one-fourth the size of the New World tropics; local ant diversity in Australia's tropical rain forests is indeed reported to be lower than that of the New World (Andersen 1997). Furthermore, the size of Australia's subtropical zone is about that of North America; the local diversity of its granivorous ant assemblages is roughly comparable in the subtropical deserts of Australia and the American Southwest (Morton and Davidson 1988). However, species turnover between localities may be higher in Australian deserts (Morton and Davidson 1988; Andersen 1997), suggesting once again the importance of grain and extent in understanding patterns of diversity. Quantitative surveys within and across biogeographic regions will help clarify the role that ecoclimate zone area, as opposed to area alone, plays in shaping diversity.

The energy-speciation hypothesis posits a direct link between temperature and speciation rate (Rhode 1992; Roy et al. 1998). Our results add to the increasing variety of taxa that show a strong correlation between these two variables (Currie 1991; Rhode 1992; Wright et al. 1993; Kerr and Packer 1997; Kerr et al. 1998; Roy et al. 1998; van Rensburg et al. 2002). However, a second hypothesis, often called "species energy theory" (Wright 1983; Turner et al. 1987; Srivastava and Lawton 1998; Kaspari et al. 2000*a*), makes a similar prediction. It starts with the abundance-extinction hypothesis (i.e., N limits S) but goes on to argue that solar energy limits N in at least two ways: by limiting the rate of food production (gCarbon $\mathrm{m}^{-2}\,\mathrm{yr}^{-1}$; Rosenzweig 1968; Lieth 1975) and/or by limiting access to this food by ectothermic taxa (Turner et al. 1987; Kaspari et al. 2000*a*). Simplified, species energy theory argues that solar energy limits N and that N limits S.

Which hypothesis best accounts for variation in ground ant diversity in the New World? Two related pieces of evidence favor the energy-speciation hypothesis. First, temperature accounts for 55% of variation in Fisher's α; abundance accounts for 38%. In the stepwise regression, abundance accounts for no more than 2% of the variation in α after temperature and area. Second, two of the hottest biomes, warm deserts and lowland rain forests, yield the highest α's per unit abundance. The current evidence then best supports the hypothesis that temperature mainly enhances diversity not by enhancing productivity but by enhancing evolutionary rates of diversification.

However, this accruing evidence for the energy-speciation hypothesis fosters the demand for a more thorough understanding of its cause(s). Its assumptions that warmer environments generate more mutations and more sexual recombination per capita and that these limit speciation rates (Rhode 1992) remain largely untested. For example (and unlike the sampling, abundance-extinction, and area hypotheses), the energy-speciation hypothesis cannot even give us the sign of the second derivative for the temperature-diversity curve, but this may soon change (J. Gillooly, personal communication).

In sum, three-fourths of the variation in local diversity at geographical extents is accounted for by hypotheses that focus on net diversification rates, which is consistent with Ricklefs's (1987) hierarchy hypothesis. This does not discount the importance that niche differences may play in sorting species within communities along gradients of insolation (Brian and Brian 1951), moisture (Kaspari 1993), vegetation structure (Bestelmeyer and Wiens 1996; Longino and Colwell 1997; Feener and Schupp 1998), predator-free space (Franks and Bossert 1983; Porter et al. 1995; Gilbert and Morrison 1997), and soil type (Johnson 1992). We do suggest that this heterogeneity does not drive biogeographic diversity gradients (Ricklefs and Schluter 1993; Rosenzweig 1995; Hubbell 2001).

Invasive Ants

The impact of invasive species is sensitive to the scale at which it is analyzed (Levine 2000). In bait surveys of old fields and nearby forests along the eastern coast of North America, Gotelli and Arnett (2000) report a latitudinal peak in diversity at just north of the northernmost expansion of *Solenopsis invicta*. Our studies of natural areas north and south of the *S. invicta* invasion front showed little evidence of such a trend (table 2) on the basis of extensive surveys that include hand collecting, nest collections, and baits. In fact, our most diverse site in North America (Torreya State Park, Fla.) is a 2,600-ha forest embedded in a landscape that has supported *S. invicta* for >40 yr. This is not to deny the impact of *S. invicta* and other invasive ants in the localities in which they occur (Ward 1987; Porter 1988; Human and Gordon 1997; Holway 1998; Gotelli and Arnett 2000; Kaspari 2000). However, it does emphasize the fact that species range maps do not imply uniform densities of individuals. Furthermore, our data suggest that North America's ant biodiversity endures, often in pockets of undisturbed habitat. These populations will hopefully continue to be available to recolonize infested areas if and when biocontrol, natural or otherwise, succeeds (Porter et al. 1995; Gilbert and Morrison 1997; Orr and Seike 1998; Morrison 2002).

Ecologists have long known that patterns of diversity are sensitive to spatial scale (Elton 1927; Preston 1962). A deeper exploration of the processes underlying those scaling laws is now under way (Ricklefs and Schluter 1993; Brown 1995; Rosenzweig 1995; Hubbell 2001; Lomolino and Weiser 2001). A vital step in this process is the careful quantification of diversity gradients at different grains and extents (Fraser 1998; Waide et al. 1999; Losos and Schluter 2000; Crawley and Harral 2001; Lyons and Willig 2002; van Rensburg et al. 2002). Through this combination of theory and fieldwork, ecologists will forge the next generation of biodiversity scaling laws.

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