

# Energy, Density, and Constraints to Species Richness: Ant Assemblages along a Productivity Gradient

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**ABSTRACT:** Species richness describes the number of species of a given taxon in a given time and space. The energy limitation hypothesis links the species richness of consumer taxa to net primary productivity (NPP) through two relationships: NPP limits a taxon's density, and taxon density limits species richness. We study both relationships with a survey of 15 ground ant assemblages, along a productivity gradient from deserts to rain forests. Ant density (colonies  $m^{-2}$ ) was a positive, decelerating function of net aboveground productivity (NAP). A stepwise regression suggests that the efficiency with which NAP is converted to ant colonies increases with maximum summer temperature and decreases with precipitation. Ant species richness was a positive decelerating function of density at three spatial scales. This supports the energy limitation hypothesis' assumption that average population densities are higher in environments that are more productive. These two nonlinear functions (NAP-density and density-species richness) combine to create, at a variety of scales, positive, decelerating, productivity-diversity curves for a common, ecologically dominant taxon across the terrestrial productivity gradient. However, variance in the density and diversity explained by NAP decreases with scale, suggesting that energy limitation of diversity predominates at small spatial scales ( $<1$  ha).

**Keywords:** diversity, net primary production, efficiency, taxon, climate.

A central question in ecology is how community properties change as one travels from place to place across the planet

(Clements 1916; Whittaker 1970; MacArthur 1972; Orians and Pearson 1983; Pianka 1986; Schluter 1986; Menge and Sutherland 1987). One such property is species richness ( $S$ ): the number of species found in a given area, over a given amount of time, in a given taxon. Energy availability has long been considered a fundamental constraint to species richness (Hutchinson 1959; Connell and Orias 1964; Paine 1966). In the energy limitation hypothesis, the rate that energy enters a system limits the species richness of a consumer taxon by limiting the density of its individuals (Wright 1983; Currie 1991; Wright et al. 1993; Rosenzweig 1995; Siemann 1998; Srivastava and Lawton 1998).

The energy limitation hypothesis posits that a consumer taxon's  $S$  is regulated in a two-step process. First, energy enters a habitat as net primary productivity (NPP;  $gC\ m^{-2}\ yr^{-1}$ ), the total gross carbon uptake of  $CO_2$  by plants (i.e., gross primary productivity [GPP];  $gC\ m^{-2}\ yr^{-1}$ ) less total plant respiration ( $gC\ m^{-2}\ yr^{-1}$ ). As the habitat's NPP increases, so does its ability to support more individuals of that taxon—the taxon's density ( $D$ ). Second, as  $D$  increases, more species of that taxon can exist at a given population size (conversely, as the number of individuals decreases, population size decreases, and local extinction rates increase, lowering  $S$ ). The energy limitation hypothesis thus posits that a taxon's density is limited by a habitat's productivity, and a taxon's species richness is limited by its density (see also Srivastava and Lawton 1998).

The energy limitation hypothesis is often used to explore how species richness, measured over large areas (e.g.,  $1^\circ \times 1^\circ$ ; Currie 1991), varies geographically (Rosenzweig 1995). However, key elements of this hypothesis (e.g., resource competition and population extinction) occur at local (e.g., 1 ha) scales. Moreover, patterns of local species richness can sum to create diversity gradients at larger scales (e.g., increased landscape relief enhances species richness measured at the  $1^\circ \times 1^\circ$  scale; Kerr and Packer 1997). Our focus here is the geographic distribution of local species richness (e.g., Pianka 1975). We know of no tests of the energy limitation hypothesis that study local richness across the terrestrial productivity gradient.

Wright et al. (1993) argue that the energy limitation

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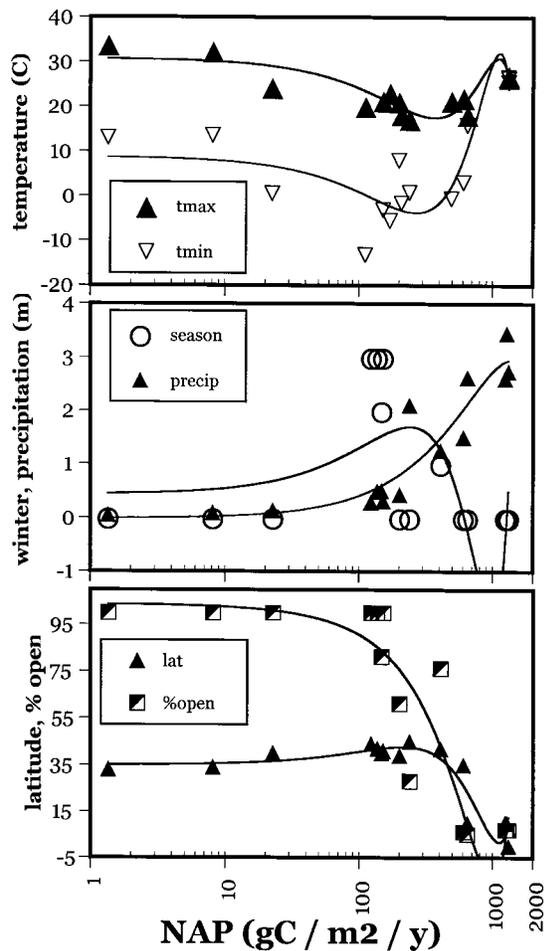


Figure 1: Climate, latitude, and vegetation structure vary along a gradient of net aboveground productivity (NAP). Estimates of canopy cover at 1.5 m by use of a spherical densiometer represent “% open.” Season is the number of months that average temperature is below 0°C. Precipitation and minimum/maximum (*tmin/tmax*) temperatures are from local records. Lines are best-fit polynomial regressions and are purely descriptive.

hypothesis is the best supported of the major theories for gradients in species richness, given diversity’s often positive correlation with productivity, especially measured at large spatial scales. Rosenzweig and Abramsky (1993), in the same volume, suggest that energy limitation commonly gives way to other mechanisms that depress species richness, forming a unimodal relationship between productivity and diversity. Regardless, correlations between productivity and diversity are only a first step in testing the energy limitation hypothesis.

Few studies have considered how energy is captured and partitioned among individuals of a taxon, yielding the relationship between productivity and density (Brown 1981;

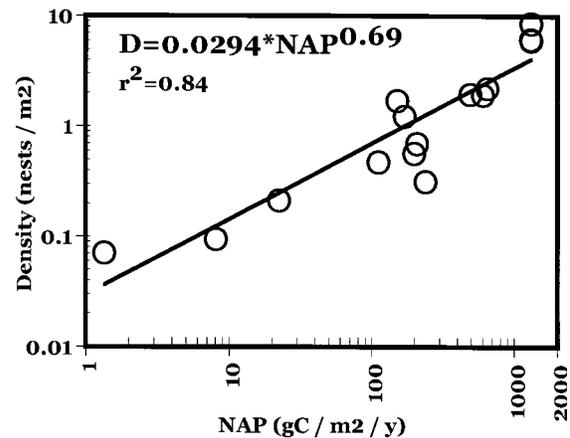


Figure 2: Density of ground-nesting ants increases with net aboveground productivity. The exponent  $0 < 0.69 < 1$  describes a positive decelerating relationship.

Abrams 1995). One promising model (OFAN; Fretwell 1977; Oksanen et al. 1981; Power 1992) argues that the accumulation of trophic levels along a productivity gradient may cause the biomass of a single trophic level to first accrue and then plateau as it is sequentially limited by resources and predators. This produces a signature staircase of biomass and density along a productivity gradient (e.g., Kautzinger and Morin 1998). Likewise, abiotic factors have been linked, not just to plant productivity, but to the ability of consumers to harvest productivity (Andrewartha and Birch 1954). However, we know of no studies of taxon density along the terrestrial productivity gradient, nor any that dissected the impact of productivity on taxon density from its covariate, temperature. Srivastava and Lawton (1998) found little evidence for a relationship between productivity and density in a series of artificial tree holes in a British forest. The energy limitation hypothesis’ second part—the limitation of species richness by taxon density—is also poorly understood. Verbal models (e.g., Rosenzweig 1995) implicitly assume a positive correlation between density and richness; Srivastava and Lawton (1998) suggest a logarithmic or power function. However, density-species richness (*D-S*) curves, built from a variety of wide habitats and densities, have yet to be constructed.

In summary, the energy limitation hypothesis—currently being used to explore the pattern and mechanics of diversity within habitats (Siemann et al. 1996; Siemann 1998; Srivastava and Lawton 1998)—offers opportunities for such insights between habitats at geographic scales (Abrams 1995; Rosenzweig 1995).

**Table 1:** Description of 15 sites surveyed for this study

Site	Long. (°W)	Lat. (°N)	Net aboveground productivity	% open	Date	Dominant species (no. recorded) <sup>a</sup>	Habitat
East Mesa Geothermal Site	116	33	1.4	100	4/94	<i>Pogonomyrmex magnacanthus</i> (1)	Colorado Desert: creosote shrub
Deep Canyon Biological Station	117	34	8.1	100	4/94	<i>Pheidole yaqui</i> (2)	Mojave Desert: mixed shrub and cactus
Fallon Recreation Area	120	40	22.5	100	5/94	<i>Pogonomyrmex californicus</i> (3)	Great Basin Desert: sage scrub
North Great Basin Experimental Range	119	44	111.8	100	8/95	<i>Formica manni</i> (6)	Northern Great Basin Desert: sage scrub
Central Plains Experimental Range	105	41	151.7	100	8/94	<i>Dorymyrmex insanus</i> (6)	Shortgrass prairie: <i>bouteloua</i>
Arapaho Prairie	102	42	170.6	100	8/94	<i>Pheidole bicarinata</i> (6)	Sandhills prairie: <i>Andropogon</i> , <i>Bouteloua</i>
Galena Creek State Park	120	40	208.5	81	5/94 6/95	<i>Leptothorax nitens</i> (6)	Pine woodland: ponderosa pine
Cold Canyon Nature Reserve	122	39	199.3	61	4/94 5/95	<i>Tapinoma sessile</i> (4)	California coastal woodland: <i>Quercus</i>
H. J. Andrews Experimental Forest	123	44	239.3	28	8/95	<i>Stenamma</i> nr <i>sequoiarum</i> (6)	Temperate rain forest: Douglas-fir
Myles Standish State Park	72	42	493.4	76	6/95	<i>Aphaenogaster rudis</i> complex (9)	Pine barrens: white, pitch pine
Coweeta Experimental Forest	84	35	605.2	6	8/94	<i>A. rudis</i> complex (19)	Temperate mixed hardwood forest
Monteverde Reserve	83	10	649.3	5	12/95	<i>Pheidole monteverdensis</i> (12)	Tropical cloud forest
Isla Barro Colorado, Panama	80	10	1,310.2	7	6/94	<i>Cyphomyrmex rimosus</i> -1 (9)	Lowland tropical rain forest
Fort Sherman, Panama	80	10	1,318.4	7	6, 7/94	<i>Pheidole ruidum</i> (13)	Lowland tropical rain forest
Yasuni National Park, Ecuador	77	0	1,316.6	7	2, 4/95	<i>Solenopsis</i> Y1 (12)	Lowland tropical rain forest

<sup>a</sup> Lists the most common species nesting on the transect and the number of nests recorded.

### Ground Ant Assemblages along an NPP Gradient

Ants are common and key players in most terrestrial ecosystems (reviewed in Hölldobler and Wilson 1990). Although ants as a taxon include trophic specialists (e.g., detritivores, herbivores, and predators), the majority of ant species are omnivorous—exploiting nectar, capturing prey, and scavenging opportunistically (Hölldobler and Wilson 1990).

Studies linking ant diversity to productivity have yielded mixed results. In deserts, indirect measures of productivity

(rainfall) are positively correlated with *S* in North America (Davidson 1977) but not Australia (Morton and Davidson 1988) nor South America (Medel 1995). Across 129 tiny Bahamian cays, plant cover and plant diversity combined to explain 71% of variation in ant species richness (Morrison 1998). As in most diversity studies, these surveys are not directly comparable; they sampled different subsets of the fauna at different temporal and spatial scales and measured different surrogates for NPP. Here we use a standardized sampling protocol and the energy limitation hy-

**Table 2:** Stepwise multiple regression suggests that ant density is highest in warm productive habitats

Variable	Slope	Order	Partial $r^2$	Model $r^2$	$F$	$Pr > F$
Net primary productivity	.810	1	.84	.84	70.2	.0001
Maximum monthly temperature	.042	2	.08	.92	11.2	.0058

pothesis to analyze patterns of ant community structure across the terrestrial productivity gradient.

The energy limitation hypothesis posits that NPP sets an upper limit on biomass and density. However, abiotic variables also restrict access to a habitat's resources. For example, ants are small and prone to desiccation (Whitford et al. 1981; Kaspari 1993a). They are also common in warm environments; many authors suggest they are thermophiles (Brown 1973; Hölldobler and Wilson 1990; Andersen 1992). Likewise, two other gradients, latitude and potential evapotranspiration (PET;  $\text{mm m}^{-2} \text{y}^{-1}$ ), an estimate of solar input to a habitat, have been linked to animal diversity at larger scales than those in this study (Pianka 1966; Currie 1991; Ricklefs and Schluter 1993; Rosenzweig 1995). After analyzing the predictions of the energy model, we use stepwise regressions to explore how these gradients modify the effects of NPP on density and diversity.

### Methods

We studied 15 ground ant assemblages from deserts to rain forests, representing the range of productivity found in the Americas. We estimated productivity from each site by first estimating the site's actual evapotranspiration (AET;  $\text{mm m}^{-2} \text{y}^{-1}$ ) by using tables and equations of Thornthwaite and Mather (1957) and climate data from on-site weather stations and an international database (Federal Climate Complex 1995). AET reflects the amount of rainfall returned to the atmosphere and is calculated from a site's latitude, soil and vegetation type, and mean monthly temperature and rainfall. AET generally increases with a site's solar input, precipitation, and soil capacity. In a linear regression across 24 sites, Rosenzweig (1968) used  $\log_{10}$  AET to explain 90% of net aboveground productivity (NAP) in undisturbed habitats. This link between AET and productivity has justified the use of AET as a productivity surrogate in a variety of studies (e.g., Currie 1991; Rosenzweig 1995). Reanalysis of Rosenzweig's data suggested that a polynomial regression,  $\log_{10} \text{NAP} = 7.4045 + 6.0530 \times \log_{10} \text{AET} - 0.8327 \times \log_{10} \text{AET}^2$  fits the data better ( $r^2 = 0.93$ , all three terms  $P < .02$ ). We used this equation to calculate a site's net aboveground productivity ( $\text{g m}^{-2} \text{yr}^{-1}$ ) standardized in units of  $\text{gC m}^{-2} \text{yr}^{-1}$  by multiplying by 0.475 (Odum 1971). NAP focuses on the portion of productivity that is most precisely measured

(Whittaker 1970). Furthermore, output of the Rosenzweig model for these sites matches closely (Pearson's  $r = 0.9985$ ,  $n = 15$ ,  $P < .0001$ ) output from Lieth's (1976) algorithm, which correlates AET to total NPP.

All sample sites were located in protected, undisturbed habitats with native vegetation typical to the area (e.g., U.S. Long Term Ecological Research Sites, Biological Field Stations; table 1). At each site, we used a standard protocol to gather data on NPP,  $D$ , and  $S$ .

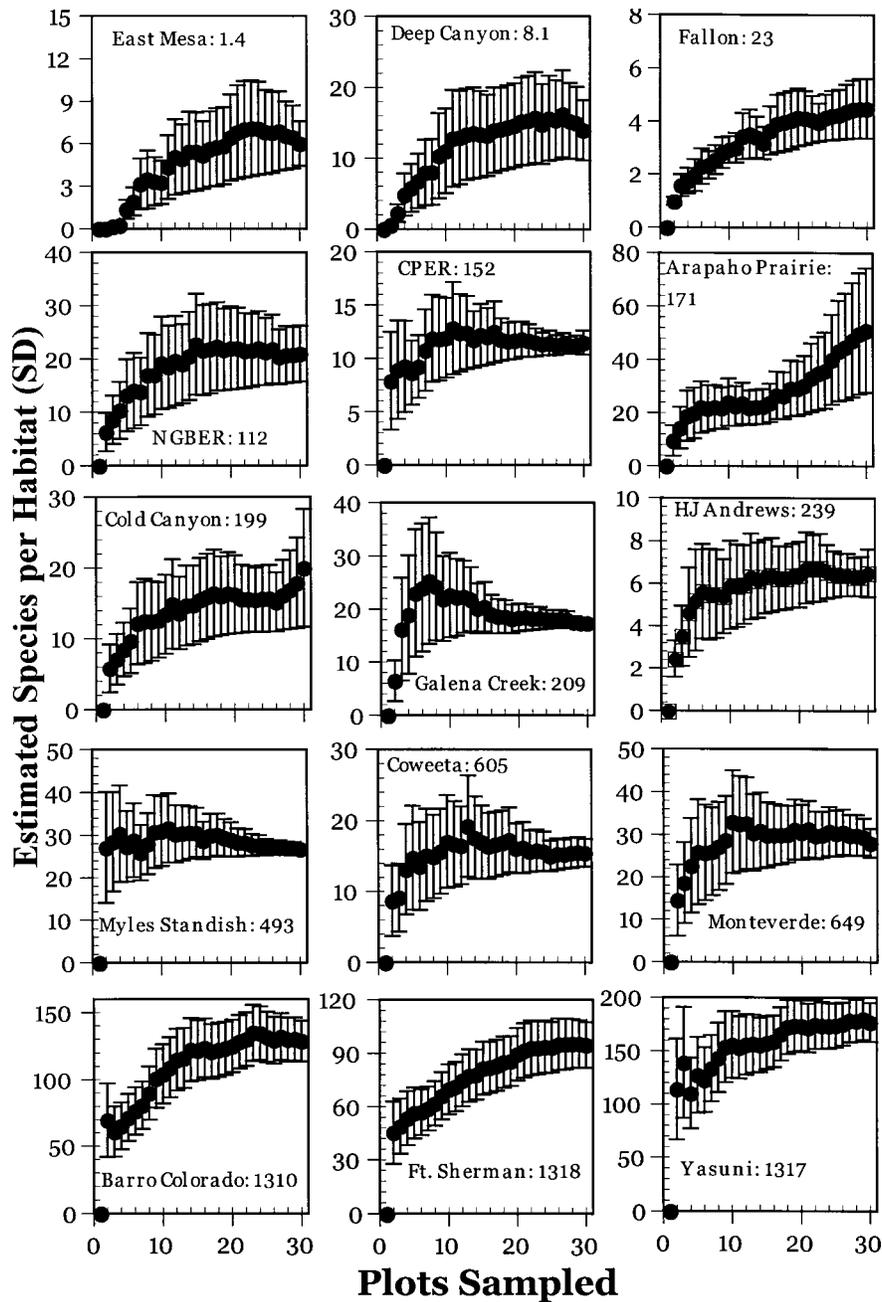
### Survey

The basic sample units in this study were 30 1-m<sup>2</sup> plots, placed in a linear transect, 10 m apart. Each 330-m transect was located in a relatively flat area by using a topographic map. Sites were sampled at times of the year with high ant activity (table 1). Transects were sampled on days neither rainy nor less than 20°C air temperature at the ground. Canopy closure (percentage open canopy) was estimated above each plot using a spherical densiometer.

Ants were sampled from each quadrant. First, any litter was inspected piece by piece for nests (ant colonies of <100 workers often nest in hollow twigs, acorns, and between leaves; Wilson 1959; Herbers 1986; Byrne 1994; Kaspari 1996). Litter was inspected over a white sample tray to catch and to locate stray ants. Litter nests were bagged for later processing. After the plot had been cleared of litter (if any), it was visually inspected for colonies and individuals and these were collected.

Later, the plot was baited with Pecan Sandies (Keebler). These shortbread cookies contain fats, carbohydrates, and proteins and are excellent ant bait (S. Cover, personal communication). The cookies can be crumbled for uniform coverage on a plot, and they contrast well against dark soil. The bait allowed us to locate cryptic nests and to sample ants foraging on the plots, but nesting off the plots.

Ants from each site were pinned and identified to species by using existing keys; identifications were checked at the Museum of Comparative Zoology, Harvard University. Specimens that could not be matched to known species were assigned to morphospecies. Vouchers are deposited at the Museum of Comparative Zoology, and a species list for each site is available from M. Kaspari.



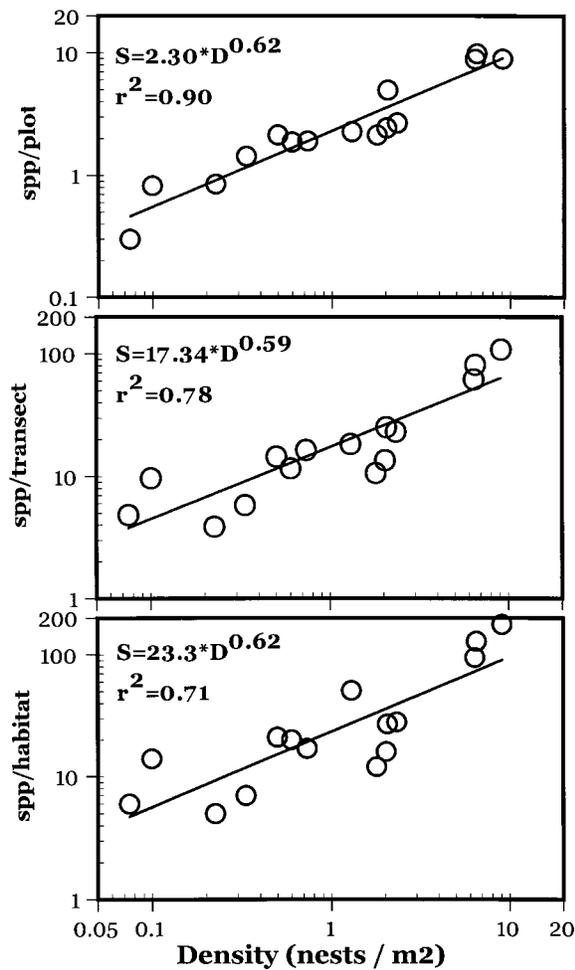
**Figure 3:** Relationship between the Chao 2 estimate of habitat species richness ( $S$ ) and the number of plots sampled in each of 15 habitats (each plot includes the net aboveground productivity [NAP] estimate,  $\text{gC m}^{-2} \text{yr}^{-1}$ , for that site). Each point is the mean of 50 randomizations. All but two sites (Arapaho Prairie and Cold Canyon; table 1) show saturating estimates of  $S$  at or before 30 plots were sampled.

*Density and Species Richness*

Density ( $D$ , ant nests  $\text{m}^{-2}$ ) was estimated from counts of nests on the 30  $1\text{-m}^2$  plots. At high-density sites, multiple nests of the same species were sometimes found in a plot. To minimize the likelihood of counting colony fragments

of the same genetic individual (and thus inflating  $D$ ), a species nest record was counted only once per plot. Densities from three low-NAP sites (East Mesa, Deep Canyon, and Fallon) were calculated using an additional 10 plots on an extended 40-plot transect.

We use three measures of local species richness. The



**Figure 4:** Species richness of ground-nesting ants at three spatial scales increases with nest density, with decreasing variance explained ( $r^2$ ) at larger spatial scales. The exponents  $0 < 0.59-0.62 < 1$  describe a positive, decelerating relationship between density ( $D$ ) and species richness ( $S$ ).

average number of species found in a  $m^2$  plot is  $S_{\text{plot}}$ . The summed number of species collected from the 30 plots spanning 330 m is  $S_{\text{transect}}$ . An estimate of the total number of species in the site assuming that our sampling had gone to completion is  $S_{\text{habitat}}$  (the Chao 2 statistic; Colwell and Coddington 1994). As such estimators are sensitive to sample size, we used EstimateS (Colwell 1997) to build 50 randomized accumulation curves with which to estimate the standard deviation of the estimate (Colwell and Coddington 1994). Accumulation curves that plateau suggest a complete sample. These three measures,  $S_{\text{plot}}$ ,  $S_{\text{transect}}$ , and  $S_{\text{habitat}}$ , sample species richness at increasing spatial scales (although Chao 2 is spatially ambiguous; Colwell and Coddington 1994).

### Statistics

The basic analysis tool in this study was least-squares linear regression (SAS 1988) on log-transformed data, yielding exponential relationships of the form  $y = ax^b$ . We used least squares linear regression (SAS 1988) to test for causal relationships between variables, and ancillary  $F$ -tests to test of linearity in slopes (i.e.,  $aN^x$ , where  $x = 1$ ). After these tests, we ran stepwise regressions (criteria for inclusion and exclusion,  $P < .05$ ) to explore how other variables may modify the relationships between density, diversity, and productivity. We used the following variables: temperature (monthly maximum and minimum), number of months with average temperature less than  $0^\circ\text{C}$ , percentage open canopy, latitude, annual precipitation, and potential evapotranspiration (PET). The last two were log-transformed to fit normality assumptions. We also report the results of individual linear regressions between diversity and these variables.

### Results

We sampled 15 sites that varied three orders of magnitude in NAP. NAP did not vary consistently with latitude, temperature (maximum or minimum), or seasonality (fig. 1). Sites that are more productive were also wetter on average.

Physiognomy of the 15 sites varied dramatically (fig. 1; table 1; see Kaspari 2000 for photographs of the sites). Low productivity habitats lacked trees (100% open canopy) from deserts ( $1.4-111.8 \text{ gC m}^{-2} \text{ yr}^{-1}$  to short and mixed grass prairie ( $151.7-170.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ ), all  $>100^\circ \text{W}$ . Canopy cover became patchy (61%–81% open) through pine and pine-oak woodlands ( $199.3-493.4 \text{ gC m}^{-2} \text{ yr}^{-1}$ ). The canopy closed in temperate rain forests and tropical cloud forest sites ( $239.3-649.3 \text{ gC m}^{-2} \text{ yr}^{-1}$ ) that were considerably darker and cooler than woodlands with similar productivity. Mixed hardwood temperate forest and three tropical lowland forests completed the gradient ( $605.2-1316.6 \text{ gC m}^{-2} \text{ yr}^{-1}$ ). Ground cover increased from desert pavement, to closed grassland with litter patches, to a uniform litter layer.

A total of 2,268 ant records and 323 species were recorded from the 15 sites. Of these, 1,275 (56%) of the records and 230 (71%) of the species came from the four tropical forests. Many tropical species (131 or 57%) could not be matched with certainty to specimens at the Museum of Comparative Zoology, and these were assigned morphospecies. The same was true for two (2%) of the temperate species. Only two of the 15 sites shared a numerically dominant nesting species (*Aphaenogaster rudis* complex, table 1). Generally, ants from low-NAP sites nested in soil. As canopies closed and litter accumulated, more ants nested in hollow twigs and pieces of dead wood.

**Table 3:** Simple linear regressions of density, productivity, five ecoclimatic variables, and latitude on ant species richness at three spatial scales

Variable	m <sup>2</sup>		Transect		Habitat	
	r <sup>2</sup>	Sign	r <sup>2</sup>	Sign	r <sup>2</sup>	Sign
Density	.90 <sup>***</sup>	+	.78 <sup>***</sup>	+	.70 <sup>***</sup>	+
NAP	.85 <sup>***</sup>	+	.58 <sup>***</sup>	+	.51 <sup>**</sup>	+
Precipitation	.72 <sup>***</sup>	+	.53 <sup>**</sup>	+	.45 <sup>**</sup>	+
PET	.09 <sup>NS</sup>	+	.24 <sup>NS</sup>	+	.19 <sup>NS</sup>	+
Months ≤0	0 <sup>NS</sup>	+	0 <sup>NS</sup>	−	0 <sup>NS</sup>	−
Maximum monthly temperature	.05 <sup>NS</sup>	−	0 <sup>NS</sup>	+	.01 <sup>NS</sup>	+
Minimum monthly temperature	.17 <sup>NS</sup>	+	.36 <sup>*</sup>	+	.33 <sup>*</sup>	+
Latitude	.36 <sup>*</sup>	−	.60 <sup>***</sup>	−	.55 <sup>**</sup>	−

Note. PET = potential evapotranspiration; NAP = net aboveground productivity.

<sup>NS</sup>  $P > .05$ .

<sup>\*</sup>  $P < .05$ .

<sup>\*\*</sup>  $P < .01$ .

<sup>\*\*\*</sup>  $P < .001$ .

#### *Productivity Limitation of Density: The NAP-D Curve*

Ground ant densities spanned two orders of magnitude, from  $D = 0.075$  nests m<sup>-2</sup> in the Colorado desert to  $D = 9.1$  nests m<sup>-2</sup> in the Ecuadorian lowland rain forest (fig. 2). NAP explained 84% of the variation in density in a log<sub>10</sub> linear regression ( $F = 70.24$ ,  $df = 1, 14$ ,  $P < .0001$ ). The slope of the line was significantly  $< 1$  ( $H_0$  slope = 1:  $F = 14.6$ ,  $df = 1, 13$ ,  $P < .002$ ).  $D$  varied almost an order of magnitude at NAPs between 100 gC m<sup>-2</sup> yr<sup>-1</sup> and 300 gC m<sup>-2</sup> yr<sup>-1</sup> (fig. 2). There was no suggestion of an OFAN staircase between NAP and  $D$  (verified with a polynomial regression—quadratic and cubic factors  $P > .40$ ). In a stepwise regression, only maximum monthly temperature was further positively correlated with density. It accounted for an extra 8% of the variance in  $D$  (table 2).

#### *Density Limitation of Species Richness: The D-S Curve*

The species richness ( $S$ ) of ground-nesting ants ranged over 1.5 orders of magnitude at each scale (fig. 3, 4). The values of  $S_{\text{plot}}$  (mean species m<sup>-2</sup>) ranged from 0.3 (Colorado Desert) to 9.8 (Panamanian moist rain forest). The values of  $S_{\text{transect}}$  (species 30 m<sup>2</sup> plots along a 330 m transect) ranged from 4 (Colorado and Great Basin Desert) to 112 (Ecuador lowland rain forest). Estimates of  $S_{\text{habitat}}$  saturated and standard deviations stabilized, and/or converged, in 13 of 15 sites (fig. 3). Further sampling in those sites would have likely added no more species. The values of  $S_{\text{habitat}}$  ranged from 5 (Great Basin desert) to 177 (Ecuador lowland rain forest). Measures of  $S$  were highly correlated, with the strongest correlations among the two larger scales (Pearson's  $r_{\text{transect-habitat}} = 0.97$ ,  $r_{\text{plot-transect}} = 0.92$ ,  $r_{\text{plot-habitat}} = 0.89$ , all  $P < .0001$ ).

Assemblages with higher nest densities supported more species (fig. 4). All  $D$ - $S$  curves in log-log space had positive slopes less than unity, and hence were positive and decelerating for  $S_{\text{plot}}$  ( $F = 118.9$ ,  $df = 1, 14$ ,  $P = .0001$ ;  $H_0$  slope = 1:  $F = 45.04$ ,  $df = 1, 13$ ,  $P < .0001$ ),  $S_{\text{transect}}$  ( $F = 45.3$ ,  $df = 1, 14$ ,  $P = .0001$ ;  $H_0$  slope = 1:  $F = 22.2$ ,  $df = 1, 13$ ,  $P = .0004$ ), and  $S_{\text{habitat}}$  ( $F = 31.0$ ,  $df = 1, 14$ ,  $P = .0001$ ;  $H_0$  slope = 1:  $F = 12.05$ ,  $df = 1, 13$ ,  $P = .0041$ ).

In summary,  $D$  varied about two orders of magnitude along the terrestrial productivity gradient, and samples at larger spatial scales tallied more species. Across all scales, species richness was a positive decelerating function of nest density. The ability of density to predict variance in species richness declined with increasing scale from  $S_{\text{plot}}$  ( $r^2 = 0.90$ ) to  $S_{\text{transect}}$  ( $r^2 = 0.78$ ) to  $S_{\text{habitat}}$  ( $r^2 = 0.71$ ).

#### *Productivity and Species Richness: The NAP-S Curve*

Species richness was highest in the most productive habitats. At the plot scale,  $S$  was a positive, decelerating function of NAP ( $F = 74.3$ ,  $df = 1, 14$ ,  $P = .0001$ ;  $H_0$  slope = 1:  $F = 111.2$ ,  $df = 1, 13$ ,  $P = .0001$ ) as was  $S_{\text{transect}}$  ( $F = 18.2$ ,  $df = 1, 14$ ,  $P < .001$ ;  $H_0$  slope = 1:  $F = 48.0$ ,  $df = 1, 13$ ,  $P < .0001$ ) and  $S_{\text{habitat}}$  ( $F = 13.7$ ,  $df = 1, 14$ ,  $P = .0027$ ;  $H_0$  slope = 1:  $F = 32.6$ ,  $df = 1, 13$ ,  $P < .0001$ ). Like the  $D$ - $S$  curves, the explanatory power of NAP eroded with increasing scale (m<sup>2</sup> plot:  $r^2 = 0.85$ , transect:  $r^2 = 0.58$ , habitat:  $r^2 = 0.51$ ).

Many factors have been linked to diversity gradients. The energy limitation hypothesis, if true, predicts that density should be the best single predictor of diversity and that the productivity-diversity correlation arises from the intervening effects of density. To get a better sense of how local ant diversity matches up to other diversity correlates,

**Table 4:** Stepwise multiple regression suggests that ant diversity is highest in habitats supporting high colony densities

Variable	Slope	Order	Partial $r^2$	Model $r^2$	$F$	$Pr > F$
Number of species per square meter plot:						
Density (nests $m^{-2}$ )	.619	1	.90	.90	118.9	.0001
Number of species per 300-m transect:						
Density (nests $m^{-2}$ )	.634	1	.78	.78	45.27	.0001
Maximum monthly temperature ( $^{\circ}C$ )	.025	2	.08	.86	6.5	.0255
Estimated number of species per habitat:						
Density (nests $m^{-2}$ )	.673	1	.71	.71	31.0	.0001
Maximum monthly temperature ( $^{\circ}C$ )	.031	2	.10	.81	6.3	.0277

we first performed linear regressions between  $D$ , NAP, PET, minimum and maximum monthly temperature, precipitation, number of months  $<0^{\circ}C$ , and one geographic correlate—latitude (table 3). In each case, density predicted at least an additional 14% of the variation. The second most successful single variables were NAP (at the square meter scale) and latitude (at the transect and habitat scale).

Next, this variable set was entered into stepwise regression, which accounts for covariance among independent variables (table 4). Density remained the sole variable predicting diversity at the square meter scale, and maximum monthly temperature accounted for an additional 8% and 10% of variance in diversity at the larger scales. Thus, when density was (statistically) held constant, warmer habitats had more ant species at larger scales.

### Discussion

Geographic gradients in local species richness have long fascinated ecologists (Dobzhansky 1950; Hutchinson 1959; Pianka 1966; MacArthur 1972; Rosenzweig 1995). At the local (e.g., 1 ha) scale,  $S$  has been shown to increase with habitat heterogeneity (MacArthur et al. 1962), the size of the regional species pool (Ricklefs 1987; Ricklefs and Schluter 1993), and, at least temporarily, with time since disturbance (Whittaker 1970; Odum 1971). This article develops and tests the energy limitation hypothesis (Connell and Orias 1964; Brown 1981; Wright 1983; Rosenzweig 1995) by using the three order of magnitude terrestrial productivity gradient—the first study we know of to do so. Consistent with the energy limitation hypothesis, density increased with NPP, and species richness increased with density. However, neither curve was linear and both decelerated, adding colonies and species at a slower rate with higher productivity. Here we review some mechanisms that may produce these curves.

First, we address two potential biases in our sampling protocol. The first was our failure to sample for arboreal ants. Ants may make up most of the canopy animal biomass in lowland tropical forests (Tobin 1991; Stork and

Blackburn 1993; Davidson 1997) but rarely nest in the canopy of the temperate sites sampled (Jeanne 1979; S. Cover, personal communication; M. Kaspari, personal observation). Quantitative methods for sampling the canopy are in their infancy, as are methods of combining the ground and canopy fauna to characterize communities (Longino and Colwell 1997). If we exclude the five communities with a known canopy fauna (Coweeta and the four tropical sites), the slope of the curve does not rebound—as predicted if canopy fauna significantly contributed to density. Instead the exponent drops from 0.69 to 0.61 ( $D = 0.038NAP^{0.61}$ ,  $r^2 = 0.80$ ).

Second, our tests use net aboveground productivity (NAP), which ignores belowground primary production. Belowground measures of productivity are notoriously difficult (Whittaker 1970). Although our estimates of NAP correlate closely ( $r = 0.99$ ) to a second model linking total NPP to AET (Lieth 1976), many total NPP estimates arrive from simply doubling estimates of NAP. If below ground production varies nonlinearly with aboveground production, and/or if ant assemblages vary in their use of belowground resources along the NPP gradient, then figures 3–5 may vary commensurately.

### NAP-D

The local density of ants varied over two orders of magnitude across the terrestrial NAP gradient, reaching its apex in the lowland Tropics. Yet the increase was saturating, suggesting that ants as a taxon store less of the available annual energy at a site at more productive sites. After Odum (1971), we suggest that NAP- $D$  curves arise from gradients in the ability of a taxon to harvest and sequester energy.

### Gradients in Harvesting Energy

In the intertaxon competition hypothesis, Rosenzweig and Abramsky (1993) proposed that taxa vary in their ability to capture energy along the productivity gradient. This

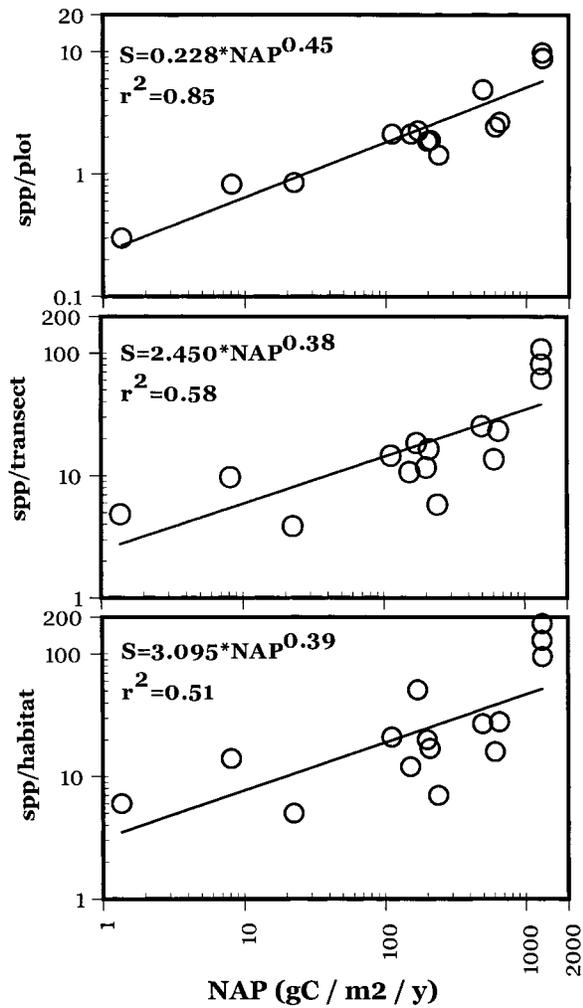


Figure 5: Species richness ( $S$ ) at three spatial scales is a positive, decelerating function of net aboveground productivity (NAP), with decreasing variance explained ( $r^2$ ) at larger spatial scales. The exponents  $0 < 0.38-0.45 < 1$  describe a positive decelerating relationship between NAP and  $S$ .

ability, which we call the “taxon efficiency,” describes the realized conversion of a habitat’s primary production into a taxon’s individuals. Unimodal productivity-diversity curves, Rosenzweig and Abramsky argue, arise when taxon efficiencies are staggered along the NAP gradient.

We estimated taxon efficiency here as the density of ants per unit NAP. This measure varied over an order of magnitude, from 0.001 (in the temperate rain forest) to 0.08 (in the most arid desert). Regressed against NAP, it gave a significantly negative slope ( $0.03 \text{ NAP}^{-0.31}$ ), explaining half the variance ( $r^2 = 0.53$ ,  $F = 14.6$ ,  $df = 1, 14$ ,  $P < .003$ ). In other words, ground ants converted the largest fraction of a habitat’s productivity to colonies in the most depau-

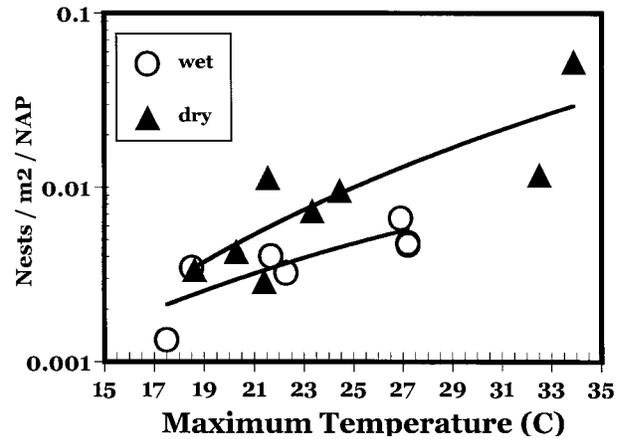


Figure 6: Taxon efficiency, the ratio of a habitat’s nest density to its productivity, increases with the maximum monthly temperature and decreases with precipitation. For illustrative purposes, habitats are grouped as dry ( $< 0.5 \text{ m yr}^{-1}$ ) and wet ( $> 1.4 \text{ m yr}^{-1}$ ).

perate habitats but were most abundant in the most productive habitats. A stepwise regression (table 5; fig. 6) suggests that two abiotic variables, maximum monthly temperature and precipitation, were positively and negatively correlated with the taxon efficiency (61% and 17% of variation explained). This supports the long-stated dictum that ants as a taxon are thermophilic (Brown 1973; Andersen 1991; Weseloh 1995). Given the importance of humidity in facilitating ant foraging at a local scale (Whitford and Ettershank 1975; Kaspari 1993a), this negative correlation with foraging efficiency at the global scale is intriguing.

#### Gradients in Sequestering Energy

Once harvested, energy is lost through mortality, metabolic heat, and excreta (Odum 1971). The deceleration in the NAP- $D$  curve may result if any of these factors increases proportionate with a habitat’s productivity. We suggest two candidates.

High NAP habitats, like the tropical forests, support Ectoninae and Cerapachyinae, ants which prey on other ants (Wilson 1958; Rettenmeyer et al. 1983; Kaspari 1996). Intrataxon predation transfers energy imperfectly from one species within the taxon to another (Polis 1988; Polis et al. 1989). Thus increasing within-taxon predation may decrease the per-capita efficiencies of a taxon assemblage (Case 1975) and, by decreasing biomass, decrease density.

Ant worker size (Cushman et al. 1993) and colony size (Kaspari and Vargo 1995) both tend to decrease toward the Tropics and, more generally, with increasing NAP (M. Kaspari, unpublished data). Smaller ants, with their higher

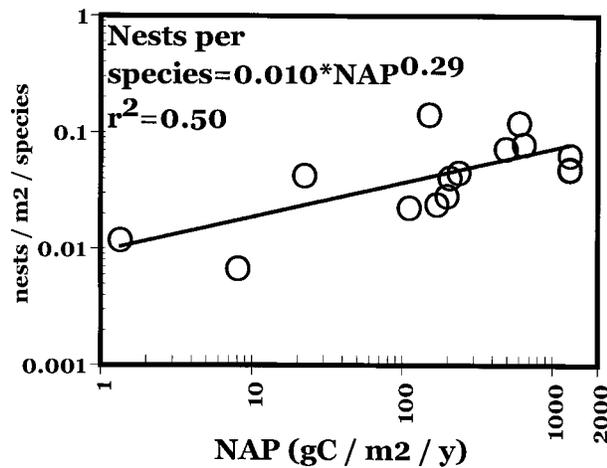


Figure 7: Average density of an ant species increases with the productivity of the habitat in which it is found. The exponent  $0 < 0.29 < 1$  describes a positive, decelerating relationship between net aboveground productivity (NAP) and average density of a species.

surface area to volume, may lose proportionately more energy as metabolic heat than similar biomass of larger individuals. Thus, ant assemblages studied here may be harvesting the same proportion of NAP from their habitats, but tropical assemblages may be losing that energy at a higher rate, as heat.

In summary, ant density increases smoothly with productivity, a key element of the energy limitation hypothesis. However, it also decelerates, which may be caused by a number of other variables, including decreased food quality, increased metabolic costs, and/or increased predation. Regardless, the shape of NAP- $D$  curves for ants are of interest to a variety of organisms. For example, the density of ant colonies in a habitat will determine the availability of the ants that tend plant nectaries, guard them from herbivores, and depredate and disperse their seeds (Tilman 1978; Beattie 1985; Kaspari 1993b).

#### Density and Species Richness

Along the New World NAP gradient, local ant species richness ranged over 1.3 orders of magnitude (fig. 4). How confident are we that these samples were unbiased estimates? The two smaller sampling scales ( $m^2$  plot, transect) were absolute species counts.  $S_{\text{habitat}}$ , the one estimate sensitive to sample size (Colwell and Coddington 1994), saturated in 13 of 15 sites sampled including four tropical rain forests (fig. 3). Increasing sample sizes beyond the 30 plots used in this protocol would likely not have increased our estimates of  $S_{\text{habitat}}$ . In the two sites where  $S_{\text{habitat}}$  did not plateau, the randomly located transects climbed a gen-

tle slope, summing over valley, slope, and ridge species (M. Kaspari, personal observation). We thus conclude that the gradient of local ant species richness was relatively unbiased, especially given the large NAP gradient sampled.

Because species richness was a positive decelerating function of density, habitats accrued species at a slower pace as density increased. These data allow us to test a fundamental assumption of the energy limitation hypothesis—that average population density increases with NAP. Calculated as density divided by  $S_{\text{habitat}}$ , average population density increases in a positive decelerating fashion with NAP ( $F = 13.2$ ,  $df = 1, 14$ ,  $P = .003$ ;  $H_0$ : slope = 1:  $F = 76.3$ ,  $df = 1, 13$ ,  $P < .0001$ ; fig. 7). Furthermore, stepwise regression analysis found no variables that explain more variation in average population density than NAP. If the average abundance of an ant species decreased in the Tropics (as it must almost certainly do for trees; Dobzhansky 1950) we would expect this curve to accelerate. Thus, the addition of rare ant species as NAP increases is more than made up for by the increase in densities of common ant species (table 1).

#### Does Density Regulate Diversity or Does Diversity Regulate Density?

May (1975) noted that density and species richness are two fundamental properties of taxa in a local community. The energy limitation hypothesis posits a causal connection between the two based on a set of propositions: local habitats are embedded in regions that determine the pool of available species (Ricklefs 1987); these species colonize the habitat, exist for a time as populations, then go extinct (Holt 1993); and higher population densities postpone this extinction (Richter-Dyn and Goel 1972; Spiller et al. 1998). Thus, increasing a taxon's density in a habitat increases the chance it will support more viable species populations for longer periods (Preston 1962; Levinton 1979; Rosenzweig 1995). For a given regional pool of species, increasing density should increase species richness.

However, an alternate scenario, which we call the "niche limitation hypothesis," also predicts a positive correlation between density and richness but reverses the causality. It starts by assuming that members of a species pool are specialized to different parts of the resource spectrum (MacArthur 1972). As the available species pool increases, so then does the taxon's ability to turn available resources into individuals (Diamond 1970; Cody 1975). For example, experimental increases in species richness increase plant standing crop (Naeem et al. 1996; Tilman 1996).

Thus, the concave-down  $D$ - $S$  curve can also be viewed as a concave-up  $S$ - $D$  curve. Interpretations differ commensurately. The concave-down  $D$ - $S$  curve of energy limitation suggests it is progressively harder to add a species

**Table 5:** Stepwise multiple regression suggests that the efficiency with which ants convert productivity to nests increases in warm arid environments

Variable	Nests per net product productivity					
	Slope	Order	Partial $r^2$	Model $r^2$	$F$	$Pr > F$
Maximum monthly temperature ( $^{\circ}\text{C}$ )	.044	1	.61	.61	20.7	.0005
Precipitation	-.28	2	.17	.79	9.6	.0092

as you increase the energy supply and hence taxon densities. Density-limited interactions like increasing niche packing and interspecific competition may limit the survival of additional redundant species, except at higher population sizes (Diamond 1970; M. Kaspari, unpublished data).

A concave-up  $S$ - $D$  curve of niche limitation suggests that increasing population size becomes increasingly easy as the regional species pool increases. This niche limitation suggests that the size of the species pool dictates taxon density by regulating the diversity of ways that a taxon can exploit a given environment. This could happen for a number of reasons, including enhanced trophic structure leading to predator mediated coexistence (Oksanen et al. 1981; Abrams 1995; Siemann 1998) correlated with increases in habitat heterogeneity (Siemann et al. 1998) and increasing importance of intraspecific to interspecific competition (Naeem et al. 1996).

Energy and niche limitation likely combine to constrain  $D$  and  $S$  in most systems (Paine 1966). At local scales, it is possible to experimentally disentangle their effects. For example, in a north temperate grassland, fertilization treatments of  $20 \times 20$ -m plots increased plant productivity although decreasing plant diversity, a measure of environmental heterogeneity for arthropods (Tilman 1996). Arthropod density and richness increased with NPP even as plant diversity decreased, supporting the energy limitation hypothesis (Siemann 1998). However, when smaller plots were planted with one to 32 species, arthropod richness increased only weakly ( $r^2 = 0.13$ ) with plant richness and failed to vary with NPP (Siemann et al. 1998).

An alternative method of disentangling  $D$ - $S$  from  $S$ - $D$  relationships is to decrease  $S$  and observe changes in density. Such a press perturbation moves a community down the  $D$ - $S$  curve. If each species uses a unique set of resources (niche limitation in the extreme), this would leave the community in a new equilibrium lower on the  $D$ - $S$  curve. If, in contrast, the assemblage was built of redundant species or generalist species, the assemblage would recover its initial density at the lower  $S$  (density compensation; MacArthur et al. 1972; Case 1975). Intermediate results would suggest the co-action of both processes. This is likely the case for the ant assemblages studied here, although niche

limitation may play a larger role at higher densities. Desert and grassland assemblages include primarily omnivorous taxa (*Dorymyrmex*, *Formica*). Tropical assemblages, in addition to common omnivorous taxa (*Pheidole*, *Solenopsis*), include specialized fungivores (the tribe Attini), specialized predators of collembola (*Strumigenys*), and social insect predators (*Labidus*, *Neivamyrmex*, *Gnamptogenys*). In summary, the question “Does density drive diversity, or does diversity drive density in ants?” is still fresh; experiments in density compensation appear to be one key to unlocking this puzzle.

### Conclusions

The energy limitation hypothesis posits that increasing a habitat's productivity should increase its species richness. In the past 10 yr a collection of NPP- $S$  curves has accumulated, showing a diversity of pattern. Tilman and Pacala (1993) and Rosenzweig (1995) both note that one pattern is conspicuously absent, a taxon whose peak diversity is at the highest NPP. We document this pattern for ants, a conspicuous, omnivorous taxon. Such a pattern is necessary for the intertaxon competition hypothesis to work (Rosenzweig 1995). We suspect that many other arthropod taxa will also eventually be shown to have such a monotonic increase.

However, this study also suggest limitations for the energy limitation hypothesis. The best predictor of diversity in this study was always  $D$  (tables 3, 4). However, density's ability to predict diversity declines at larger scales (fig. 5). Latitude, in contrast, accounts for more variation in diversity at larger scales, as does potential evapotranspiration (PET). Currie (1991), working at the scale of  $>1^{\circ} \times 1^{\circ}$  grids, found PET to be the best predictor of animal diversity from a suite of variables similar to ours. We suggest that energy supply continues to constrain diversity at larger scales. Other factors, like landscape homogeneity (Merriam 1890; Kerr and Packer 1997), dispersal limitation (MacArthur and Wilson 1967; Davis 1986; Ricklefs and Schluter 1993), competition (Rosenzweig and Abramsky 1993), and/or disturbance (Huston 1994), by removing species, will frequently reduce diversity below the maximum set by NPP. Inspection of figure 5 suggests such a

scenario, with an upper bound of the NAP-S plot that is relatively conserved but with increasing triangular scatter from the square meter to the habitat scale. In summary, we suspect that high NPP is a necessary, but not always sufficient, cause of high ant diversity in the New World.

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