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RESEARCH ARTICLE

Taxonomic level, trophic biology and the regulation of local abundance

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ABSTRACT

1 Taxocenes — monophyletic ecological assemblages — are a key focus of macroecology. Abundance (individuals per area) is a basic property of taxocenes but has received less attention than diversity, although the two are probably related. Abundance reflects a taxocene's ability to harvest and sequester available energy and divide it among individuals. This paper explores how two properties of all taxocenes — trophic makeup and taxonomic level (e.g. genus, tribe, subfamily, family ...) — may contribute to patterns of local abundance at geographical scales.

2 Forty-nine ground ant taxocenes, in habitats ranging from New World deserts to rain forests, were surveyed along a three-orders of magnitude productivity gradient using transects of 30 1-m^2 quadrats at each site. Abundance — the number of nests per transect — varied over two orders of magnitude.

3 Over 80% of the genera collected were omnivores. However, herbivore, omnivore, and predator taxa were added to ant taxocenes in roughly 1 order of magnitude steps up the productivity gradient. Specialist detritivores were added last.

4 Net primary productivity and mean monthly temperature both consistently entered regression models predicting abundance. However, while productivity was the dominant predictor of abundance for higher taxa (families, subfamilies), temperature was the dominant predictor of abundance for lower taxa (tribes, genera). The answer to the question 'What regulates the abundance of a taxocene?' is thus sensitive to the taxonomic level of analysis.

5 These data support the following scenario. Lower taxa are abiotic specialists given the insufficient number of genomes and generations required for the exploration of the entire abiotic envelope. Higher taxa, in contrast, consist of suites of abiotic specialists arrayed along the entire productivity gradient, with access to productivity everywhere the taxon occurs. If this scenario is true, individual species may respond to global changes in temperature; the higher taxa they belong to may most respond to global changes in productivity.

Key words abundance, biogeography, climate, macroecology, New World ants, productivity, scale, taxa, taxonomy, trophic level.

INTRODUCTION

Taxocenes are collections of individuals representing a monophyletic group and found in a given area (Hutchinson, 1978). Taxocenes are basic units of investigation in macroecology and have many properties of interest to ecologists, including abundance and diversity. The abundance of a taxocene, A, reflects the number of individuals of a given taxon in a given area (e.g. acridid grasshoppers/ha, *Melanoplus* grasshoppers/m^2) at a given time. While much attention has been paid to the factors producing diversity gradients (Hutchinson, 1959; Ricklefs & Schluter, 1993; Huston, 1994; Rosenzweig, 1995), we know less, empirically or theoretically, about the processes generating gradients of abundance.

Here it is suggested that the abundance of a consumer taxocene should vary with a measure of the energy fixed by plants, the taxon's physiological ability to harvest and retain that energy, and the number of trophic steps between the taxon and that energy source (Odum, 1971; Brown, 1981). Further, the argument is developed that the roles these factors play should vary with the taxonomic level of analysis. These propositions are evaluated with data from a survey of 49 New World ground ant taxocenes. Ant taxocenes are ubiquitous, ecologically important, relatively easy to sample (Hölldobler & Wilson, 1990) and are ideal taxa with which to study ecology at multiple scales (Andersen, 1997).

Energy limitation

Net primary productivity (NPP, $gC/m^2/y$) is a site's gross plant production minus plant respiration. The NPP of a site (supplemented by imported detritus, Polis *et al.*, 1997) sets the energy available to its consumers (Connell & Orias, 1964; Brown, 1981; Kaspari *et al.*, 2000b). NPP limits abundance by limiting a taxocene's biomass, B (gC/m^2, Lindeman, 1942; Hairston *et al.*, 1960; Power, 1990). The abundance of a taxocene is thus a function of B and M, where M is the average mass (in gC) of an individual, and $A = B/M$. Gradients in abundance may arise from gradients of biomass, average mass per individual, or both.

The simplest scenario is that taxocenes do not differ in their ability to convert a site's productivity into individuals over the range of sites occupied. In this case, NPP–abundance curves should increase monotonically. The next two hypotheses discuss two ways that taxocenes may differ in their conversion efficiency across the productivity gradient (see also: Rosenzweig & Abramsky, 1993).

Trophic limitation

A taxon's trophic biology fundamentally constrains its ability to convert productivity into individuals (Lindeman, 1942; Odum, 1971). Predator taxa require at least an order of magnitude more NPP to support an individual than the trophic level upon which it feeds (Odum, 1971; Heal & MacLean, 1975). The more trophic links between NPP and a consumer taxocene, the more energy is necessary to support viable populations of its individuals. This has important implications for the trophic composition of a taxocene across the NPP gradient. If taxocene abundance is energy-limited, consumer taxocenes that occupy broad NPP gradients should show a predominance of lower trophic levels at low NPP. Higher trophic levels should accrue as NPP increases (Oksanen *et al.*, 1981; Power, 1990). Taxocenes comprised largely of predators should be under-represented at lower NPP.

Temperature limitation

A taxocene's abundance is set not only by the availability of energy, but also by abiotic conditions (*sensu* Begon *et al.*, 1996) that govern the ability to exploit this energy. A suite of biotic and abiotic factors covaries with productivity, often in non-linear fashion. For example, local terrestrial productivity is limited by the seasonal dynamics of solar radiation, precipitation and soil properties (Thornthwaite & Mather, 1957; Rosenzweig, 1968; Lieth, 1975). Increases in productivity also bring changes in plant diversity and physiognomy (Stephenson, 1990; Tilman & Pacala, 1993; O'Brien, 1998). Thus, the assumption that 'taxocenes do not differ in their ability to convert a site's productivity' is systematically violated if changing conditions change a taxocene's access to productivity along the gradient.

Temperature is a key condition regulating the abundance of terrestrial organisms (Andrewartha & Birch, 1954; Krebs, 1985). Species show physiological optima with temperature (Precht *et al.*, 1973; Schmidt-Nielsen, 1990) and in turn are influenced by prey, mutualists and competitors that also show temperature optima. As a result, isotherms have been used with great success to predict the distribution of species for a variety of taxa, including birds (Root, 1988b) and butterflies (Parmesan, 1996; Parmesan *et al.*, 1999). Ants have long been considered a thermophilic taxon, based on their ubiquity in deserts and tropical sites (Brown, 1973; Hölldobler & Wilson, 1990; Andersen, 1995; Andersen, 1997). If true, for a given NPP, we should expect higher abundances of ants in sites with higher temperatures.

Taxonomic level

The taxonomic level of analysis should further delimit the processes that regulate the abundance of a taxocene along environmental gradients. For example, the factors regulating the abundance of all mammals in an area may differ in interesting ways from those regulating the abundance of a given subtaxon (e.g. rodents, bats and cats). Relatively little attention has been paid to the sensitivity of ecological pattern to taxonomic level and our ability to scale up and down taxonomically when inferring process (but see Currie, 1991; Wright *et al.*, 1993; O'Brien *et al.*, 1998).

What happens when we 'scale up' to higher taxonomic levels of analysis? By the above logic, we sum up over more independent lineages, building taxa with a greater range of temperature optima. The range of NPP used by the taxocene should also increase, as we sum over more geographically disparate taxa. At some taxonomic resolution, the taxon occupies the entire NPP gradient.

If an increase in taxonomic level results in (1) a broader range of NPP used by the taxon and (2) the accrual of abiotic specialists, it suggests a role for taxonomic level in delimiting the processes that regulate abundance in taxocenes. At low taxonomic levels, taxa should be limited by deviations from their optimal temperature. Higher taxa, in contrast, increasingly 'solve' the abiotic constraints limiting access to NPP by collecting more and more lineages of temperature specialists. As a consequence, higher taxa stand a greater chance of maximally converting a given site's productivity to individuals. In other words, higher taxa are more likely to conform to the energy limitation hypothesis's assumption that 'taxocenes do not differ in their ability to convert a site's productivity'. If true, this predicts that the abundance of higher taxa should best follow gradients in NPP, and the abundance of lower taxa should best follow gradients in temperature.

METHODS

Forty-nine ground ant assemblages were surveyed from 1994 to 1997, including two from South America, six from Central America, and 41 from North America (Appendix 1). Mean monthly temperature and rainfall was gathered from stations on site or in nearby cities and airports (Anonymous, 1995). A site's primary productivity was estimated by first calculating its actual evapotranspiration using the equations in Thornthwaite & Mather (1957). Actual evapotranspiration was related to above-ground Net Primary Productivity (NAP) using a polynomial equation ($\log_{10}\text{NAP} = 7.4045 + 6.0530{*}\log_{10}\text{AET} - 0.8327{*}\log_{10}\text{AET2}$, $r^2 = 0.93$, Rosenzweig, 1968; Kaspari *et al.*, 2000b), standardized in units of $\text{gC/m}^2\text{/y}$ by multiplying by 0.475 (Odum, 1971). NAP focuses on the portion of productivity that is most precisely measured (Whittaker, 1970). The 49 sites ranged in estimated NAP from 1 to 1315 $\text{gC/m}^2\text{/y}$. All sample sites were from protected, undisturbed habitats with native vegetation typical to the area (e.g. United States Long-term Ecological Research Sites, Biological Field Stations).

At each site, a standard protocol was used to estimate ground ant abundance. Thirty 1-m^2 plots, 10 m apart, were laid out in a randomly placed 330 m linear transect. Sites were sampled at times of the year with high ant activity. Soil and litter nests were located by thorough search of each plot, aided by baits. Abundance was estimated from the counts of nests on the 30 1-m^2 plots. Each species had a maximal density of one nest per plot to minimize the possibility of counting the same colony twice. One transect recorded no ant colonies — it was given the arbitrary value of 0.5 nests for the 30-plot transect.

An animal's thermal budget is influenced by both convection and radiation (Porter & Gates, 1969). To test the temperature limitation hypothesis, two measures are used of a ground ant's thermal environment — a site's mean monthly temperature, and its percentage insolation at 1 m, a measure of the sun's energy reaching the ground. Percentage canopy cover at 1 m was measured at each plot with a spherical densiometer.

Statistics

Ants belong to the family Formicidae. Ant taxa were identified to subfamily, tribe and genus for the purpose of this analysis. Nomenclature corresponds to Bolton (1995). To balance the needs of statistical rigour against sample size, I used, *a priori*, taxa represented by at least 10 sampled nests. All analyses were performed with the Statistical Analysis System (SAS, 1988).

The energy limitation hypothesis's prediction of monotonically increasing NAP–abundance curves was tested by: (1) finding the productivity at which the taxon showed maximum abundance; (2) assigning that peak to the first, middle, or final third of that taxon's range of NAP occupied; and (3) using a chi-square test to test for clustering of maxima at the upper third of the NAP range. Unimodality was tested for with a polynomial regression.

To test the trophic hypothesis, Tobin (1994) was used, which classifies each genus by its dominant (and sometimes secondary and tertiary) trophic habit, including fungivore, omnivore, herbivore, carnivore and unknown. His classification was modified *a priori* in two ways. The genus *Pheidole* was classified as omnivorous, based on feeding observations in this study and studies of granivory by the genus in the moist tropics and deserts (Brown *et al.*, 1975; Davidson *et al.*, 1984; Kaspari, 1993). The fungivores were also split into herbivores (*Acromyrmex* and *Atta*) if they used freshly cut plant material as a fungal substrate, or detritivores (e.g. *Cyphomyrmex*, *Trachymyrmex*) if they used dead insects and insect dung as their fungal substrate (Weber, 1972).

To evaluate the roles of productivity and temperature in regulating abundance, I used a stepwise regression linking $\log_{10}$ abundance to three variables: $\log_{10}$NAP, mean temperature, and percentage insolation (arcsine square-root transformed). Each variable needed to account for a significant ($P < 0.05$) fraction of variance to enter and stay in the model.

To evaluate the role played by taxonomic level in the regulation of abundance, first the assumption was tested that higher taxa use wider ranges of productivity. An analysis of covariance (ANCOVA) was used with subfamily, tribe and genus as the class variable, $\log_{10}$ number of nests sampled as the continuous variable, and the range of productivities used by each taxon as the dependent variable. The outcomes from the stepwise regressions (above) were then used to correlate taxonomic level (family = 1, genus = 4) with the fraction of models in which NAP had the highest success (e.g. highest r^2) predicting abundance.

RESULTS

A total of 2032 nests was collected representing 65 genera, 27 tribes, and seven subfamilies (Table 1). Total abundance varied over two orders of magnitude. The lowest abundance was recorded in a mid-elevation temperate rain forest in the Cascade Mountains (0 nests); the high value was recorded in an Amazon rain forest in Yasuni Ecuador (187 nests). Average temperature ranged from −2 °C in mountain tundra to 27 °C in tropical rain forests. Average percentage open canopy ranged from 100% in deserts and grasslands to < 5% in tropical and temperate rain forests. Correlations between NAP and mean temperature (Spearman's $r = 0.37$) and insolation (Spearman's $r = -0.74$), were both significant ($P < 0.01$), but insolation and mean temperature were uncorrelated (Spearman's $r = -0.07$, $P > 0.6$).

Trophic effects

Omnivores accounted for 82% of nests sampled across all taxocenes (Table 2). Omnivory was the most common trophic habit in three of the four common subfamilies. Only the ponerines were represented chiefly by carnivores. A small fraction of nests, 0.7%, could not be assigned a trophic category, either because no data currently exist on the genus (Tobin, 1994), or because the identity of the species is unknown.

The trophic limitation hypothesis predicts that trophic levels should accumulate sequentially along an NAP gradient (Fig. 1). Herbivores, while rare, occur along the entire productivity gradient, from the driest desert (as the seed-harvesting *Pogonomyrmex*) to the richest lowland tropical communities (as the fungus-growing *Acromyrmex* and *Atta*). Omnivores first appear at 9 gC/m^2/y, and carnivores at 186 gC/m^2/y. It is unclear from theory where detritivores should enter along the NAP gradient, but in the ants they first appear at 649 gC/m^2/y. An analysis of covariance (Table 3) suggests that the average abundance ($P < 0.004$) as well as the accumulation of nests along the productivity gradient ($P < 0.0001$) differs among the four trophic groups. Separate regressions indicate that herbivore abundance remains relatively uniform, while omnivores, carnivores and detritivores all increase (Table 3).

Table 1 Summary of ground ant abundance across the 49 New World sites. Abundance of a taxon reflects the total number of nests sampled and its percentage contribution to the survey. Stepwise regression tested for the effects of above-ground net primary productivity (NAP), mean monthly temperature, and percent insolation on a taxon's abundance. *$P < 0.05$, **$P < 0.001$, ***$P < 0.0001$. Partial r^2s are in **bold** for the factor explaining the most variance in the model. Taxa excluded from analysis (abundance ≤ 9) but collected in the study are listed at the bottom

Taxon	Abundance		Stepwise regression						
				NAP		Temperature		Insolation	
	Nests	%	Intercept	gC/m²/y	r^2	°C	r^2	%-open	r^2
Family									
Formicidae	2032	100	−0.37	0.62***	**60**	0.02*	7	—	
Subfamily									
Dolichoderinae	65	3.2	−0.71	0.22*	8	—		0.47***	**23**
Formicinae	441	21.7	−0.62	0.58***	**47**	—		—	
Myrmicinae	1285	63.2	−0.64	0.57***	**48**	0.03***	19	—	
Ponerinae subfamily	211	10.4	−1.37	0.48***	**41**	0.04***	26	—	
Tribe									
Amblyoponini	12	0.6	−0.4	—		0.01*	**9**	—	
Attini	81	4	−0.86	0.25**	14	0.03***	**44**	—	
Blepharidattini	26	1.3	−0.48***	0.13**	9	0.02***	**37**	—	
Brachymyrmecini	50	2.5	−0.54**	0.19*	13	0.02**	**21**	—	
Camponotini	40	2	−0.30*	0.19**	**19**	—		—	
Crematogastrini	59	2.9	−0.48**	0.16*	8	0.02***	**33**	—	
Dacetini	64	3.1	0.035	—		0.02**	**26**	−0.24*	13
Dolichoderini	65	3.2	−0.71*	0.23*	7	—		0.47***	**23**
Ectatommini	54	2.7	−0.67**	0.20*	11	0.02***	**34**	—	
Formicinae	38	1.9	0.40***	—		−0.02***	**27**	—	
Formicoxenini	104	5.1	—	—		—		—	
Lasiini	308	15.2	−0.68**	0.53***	**38**	—		—	
Myrmicini	99	4.9	—	—		—		—	
Pheidolini	572	28.1	−1.26***	0.52***	21	0.05***	**47**	—	
Ponerini	144	7.1	−1.16***	0.41***	25	0.03***	**36**	—	
Solenopsidini	223	11	−1.53**	0.46**	8	0.04***	**46**	0.33*	6
Stenammini	35	1.7	0.29	—		—		−0.18*	15
Genera									
Aphaenogaster	155	7.6	0.54	—		—		−0.32*	**0.12**
Apterostigma	10	0.5	−0.10*	—		0.01**	**23**	—	
Brachymyrmex	50	2.5	−0.54*	0.19*	**21**	0.02*	13	—	
Camponotus	40	2	−0.30*	0.19*	**19**	—		—	
Crematogaster	59	2.9	−0.48*	0.16*	8	0.02***	**33**	—	
Cyphomyrmex	33	1.6	−0.51**	0.15*	10	0.02***	**33**	—	
Dorymyrmex	19	0.9	−0.09*	0.17*	11	—		0.33***	**29**
Ectatomma	23	1.1	−0.11	—		0.01*	**15**	—	
Forelius	10	0.5	−0.05	—		—		0.13**	**26**
Formica	38	1.9	0.40***	—		−0.02***	**27**	—	
Gnamptogenys	31	1.5	−0.12	—		0.02*	**17**	—	
Hypoponera	46	2.3	−0.66***	0.19**	13	0.02***	**39**	—	
Lasius	120	5.9	0.71***	—		−0.03***	**28**	—	
Leptothorax	104	5.1	—	—		—		—	
Megalomyrmex	10	0.5	−0.26*	0.07*	8	0.01***	**30**	—	
Monomorium	28	1.4	−0.01	—		—		0.13*	**8**
Myrmica	81	4	0.57***	—		0.02**	**22**	—	

(Continued overleaf)

Table 1 *continued.*

Taxon	Abundance		Stepwise regression						
				NAP		Temperature		Insolation	
	Nests	%	Intercept	gC/m^2/y	r^2	°C	r^2	%-open	r^2
Neostruma	28	1.4	0.02	—		0.01*	**14**	−0.13*	8
Odontomachus	27	1.3	−0.51***	0.14*	11	0.02***	**37**	—	
Pachycondyla	19	0.9	−0.40**	0.11*	9	0.02***	**33**	—	
Paratrechina	171	8.4	−1.2***	0.46***	**38**	0.03***	18	—	
Pheidole	417	20.5	−1.86**	0.50*	5	0.06***	**53**	0.36*	4
Pogonomyrmex	10	0.5	0.39***	−0.14***	**34**	—		—	
Ponera	42	2.1	—	—		—		—	
Prenolepis	15	0.7	—	—		—		—	
Solenopsis	185	9.1	−0.86***	0.25**	8	0.05***	**57**	—	
Stenamma	32	1.6	0.25**	—		—		−0.15*	**11**
Strumigenys	23	1.1	−0.39*	0.12*	8	0.01**	**24**	—	
Tapinoma	31	1.5	0.25*	—		−0.01*	**9**	—	
Trachymyrmex	28	1.4	−0.48**	0.14*	10	0.02***	**31**	—	
Wasmannia	26	1.3	−0.48***	0.13*	9	0.02***	**37**	—	

Taxon	Nests	%	Taxon	Nests	%	Taxon	Nests	%
Subfamily			Genus			Genus (cont.)		
Cerapachyinae	2	0.1	*Acanthognathus*	4	0.2	*Linepithema*	1	0
Ecitoninae	9	0.4	*Acromyrmex*	2	0.1	*Mycetophylax*	1	0
Pseudomyrmicinae	4	0.2	*Acropyga*	5	0.2	*Myrmecina*	6	0
			Adelomyrmex	1	0	*Myrmecocystus*	2	0
Tribe			*Amblyopone*	5	0.2	*Neivamyrmex*	2	0
Basicerotini	5	0.2	*Anochetus*	3	0.1	*Prionopelta*	7	0
Cerapachyini	2	0.1	*Atta*	1	0	*Sericomyrmex*	6	0
Ecitonini	9	0.4	*Basiceros*	2	0.1	*Smithistruma*	9	0
Myrmecinini	6	0.3	*Belonopelta*	2	0.1	*Ochetomyrmex*	1	0
Ochetomyrmecini	4	0.2	*Carebara*	2	0.1	*Octostruma*	1	0
Pheidolegtonini	6	0.3	*Cerapachys*	2	0.1	*Oligomyrmex*	4	0
Plagiolepidini	5	0.2	*Cryptopone*	1	0	*Pseudomyrmex*	4	0
Pseudomyrmecinae	4	0.2	*Dolichoderus*	4	0.2	*Rogeria*	2	0
Stegomyrmecini	1	0	*Eurhopalothrix*	2	0.1	*Simopelta*	2	0
Typhlomyrmecini	1	0	*Hylomyrma*	8	0.4	*Stegomyrmex*	1	0
			Labidus	7	0.3	*Tranopelta*	3	0
			Leptogenys	2	0	*Typhlomyrmex*	1	0

Table 2 Percentage of nests sampled in this study broken down by trophic habit of the genus for four common subfamilies, and for the entire family of ants. Omnivores represent the most common trophic habit in all subfamilies but the ponerines

	Herbivore	Omnivore	Carnivore	Detritivore
Dolichoderinae	0	100	0	0
Formicinae	1	99	0	0
Myrmicinae	1	86	6	6
Ponerinae	0	24	76	0
Formicidae	1	82	12	4

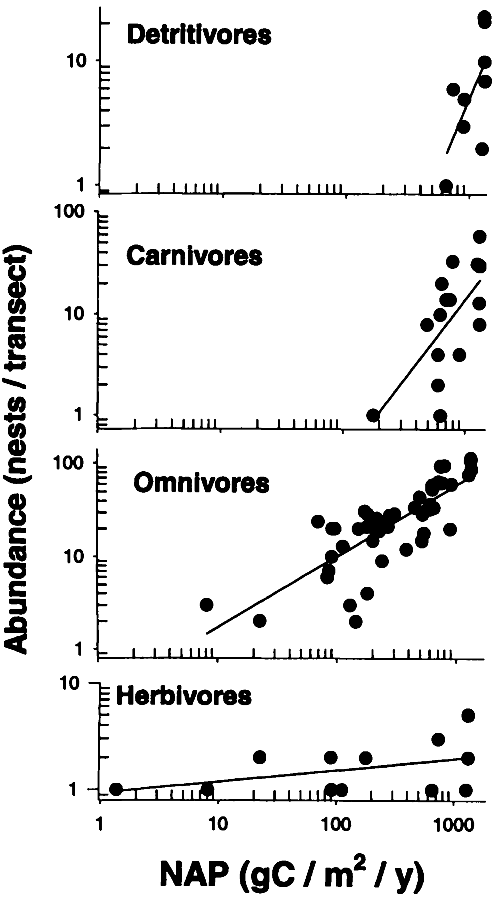

Fig. 1 The abundance of ants along the terrestrial productivity gradient, broken down by trophic category. Lines represent best fits from linear regression through non-zero points.

Energy and temperature limitation — a taxonomic analysis

Productivity–abundance curves for the New World ground ant fauna varied widely in shape within and across taxonomic resolutions. At the family level, abundance was a relatively well-defined function of productivity (Fig. 2). Four subfamilies comprise 98.5% of the ant nests sampled. Of these, the Dolichoderinae were most common at low NAP; the Myrmicinae curve mirrored that of the entire family; the Ponerinae were absent at low productivities and increased with broad scatter beyond 600 gC/m^2/y; and the Formicinae increased to a broad scatter.

Similar variation was apparent at the tribe and genus level (Fig. 3). Different tribes show patterns of peak abundance at high productivities (e.g. the Attini and Ponerini), at intermediate productivities (e.g. Myrmicini, Lasiini) and at low productivities (e.g. Formicini, Stenammini). Among the common genera, a variety of distributions were also apparent, sometimes within a single tribe (Fig. 3). For example, among the Myrmicini, there are low-, mid- and high-productivity genera (*Pogonomyrmex*, *Myrmicini* and *Hylomyrma*, respectively).

In sum, while the family Formicidae shows a basically monotonic increase in abundance with productivity, this trend breaks down at lower taxonomic levels. Two of four (50%) of the subfamilies peak in the upper third of their productivity gradient (Fig. 4), as do six of 17 tribes (35%) and 13 of 31 genera (42%). The distribution of peaks did not differ from the null hypothesis for either the tribes ($\chi^2 = 0.224$, $P = 0.89$) or genera ($\chi^2 = 1.199$, $P = 0.549$). However, simple unimodality (i.e. 'hump-shaped' productivity–abundance curves) was also uncommon. Only one subfamily (the Formicinae) and one tribe (the Lasiini) were significantly unimodal by this criterion.

The taxonomic level hypothesis assumes that subfamilies are more broadly distributed across the NAP gradient than are genera or tribes. Analysis of covariance suggests that the range of productivity occupied by these taxa differed significantly even after accounting for the number of nests sampled in the study (Table 4, Fig. 5). For example, subfamilies tended to use a range of NAP 50% larger than genera (least-square means = 1126 vs. 811 gC/m^2/y, $P < 0.0027$), but the magnitude of the difference decreased from the least to the most abundant taxa ($P < 0.0027$). When broken down by taxon, the range of NAP used by subfamilies was invariant with number of nests sampled (the Ecitoninae, a subfamily recorded only nine times and hence not included in the analysis, was found in habitats with NAP from < 200 to > 1300 gC/m^2/y, Fig. 5). In contrast, a unit increase in the number of nests sampled for genera resulted in a nearly three-fold increase in range of NAP.

The taxonomic level hypothesis predicts that temperature-related variables will be better predictors of abundance at finer levels of taxonomic

Table 3 An analysis of covariance dissects how NAP and trophic level shape abundance of ground ants across 49 sites. Linear regressions follow; in each case data are fit to a power model (for example omnivore abundance = $-0.30\text{NAP}^{0.68}$). Abundance differs across trophic levels, as does the rate that individuals accumulate on the NAP gradient. Herbivore taxa show up at smaller NAP but fail to accumulate with NAP; omnivores, carnivores and detritivore taxa show up at larger NAP and accumulate along the gradient. SS = sums of squares, MSE = mean square error, STD = standard deviation, df = degrees of freedom

Source	df	Type III SS	MSE	F	Probability of > F
NAP	1	7.37	7.37	64.83	0.0001
Trophic	2	1.91	0.96	8.40	0.0004
NAP*Trophic	2	4.69	2.34	20.61	0.0001
Error	141	16.03	0.11		

Variable		df	Estimate	STD	T	Prob > |T|
Herbivore	$r^2 = 0.02$					
Intercept		1	0.21	0.13	1.71	0.0946
NAP		1	−0.05	0.05	−0.90	0.3738
Omnivore	$r^2 = 0.62$					
Intercept		1	−0.30	0.19	−1.56	0.1267
NAP		1	0.68	0.08	8.64	0.0001
Carnivore	$r^2 = 0.33$					
Intercept		1	−1.01	0.28	−3.55	0.0009
NAP		1	0.56	0.11	4.86	0.0001
Detritivore	$r^2 = 0.24$					
Intercept		1	−0.60	0.20	−2.95	0.0049
NAP		1	0.31	0.08	3.83	0.0004

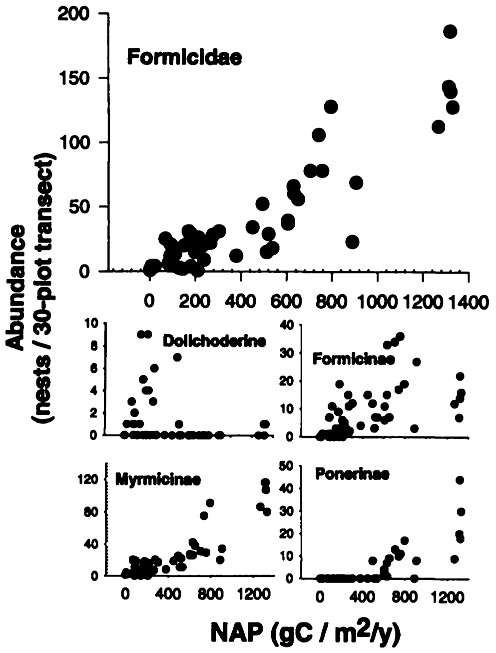

Fig. 2 Productivity–abundance curves for all ants (Formicidae) and the four most common subfamilies.

resolution. Stepwise regression was used to examine the fraction of variation in abundance explained by NAP, mean temperature and insolation for taxa from family to genera (Table 1). Productivity significantly entered the model at the family level, for four of four subfamilies, 11 of 17 tribes and 16 of 31 genera. Temperature explained significant variation at the taxon level of family, two of four subfamilies, 11 of 17 tribes and 21 of 31 genera. Insolation accounted for variation in abundance least frequently, in one of four subfamilies, four of 17 tribes and seven of 31 genera. Abundance was *uncorrelated* with the three variables in two of 17 tribes and three of 31 genera. In the majority of taxa, two of the three variables accounted for significant variation in abundance (Table 1).

Productivity's effect on abundance, when significant, was consistently positive save for one genus (*Pogonomyrmex*, harvester ants most common in deserts). As predicted by the temperature limitation hypothesis, the fraction of models in which NAP was best at explaining abundance decreased from 1.0 (subfamily) to

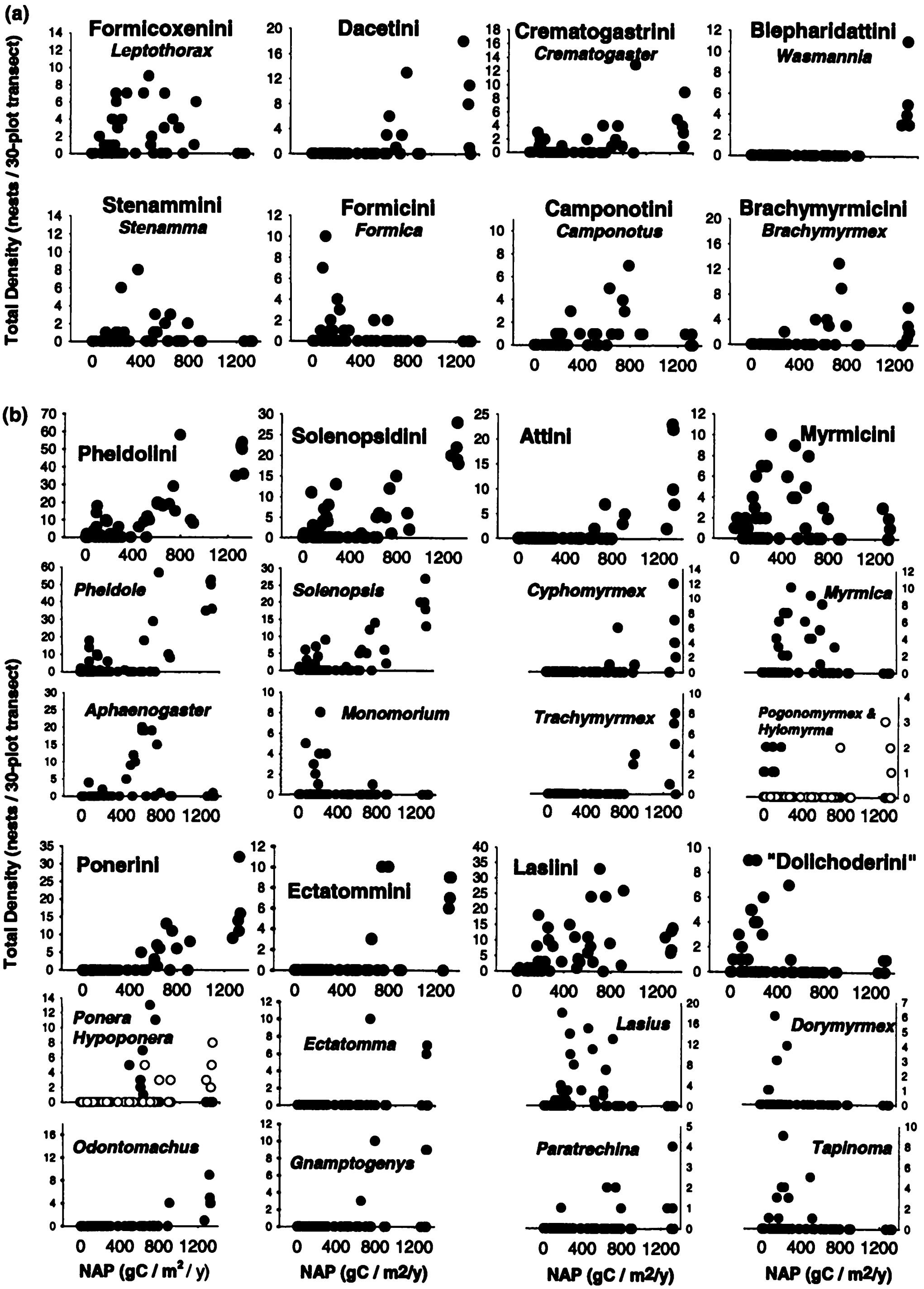

Fig. 3 Productivity–abundance curves for common tribes and genera of ants in this study. (a) Tribes with one or no common genera. (b) Tribes that include multiple common genera, with those genera shown in smaller graphs below. In two cases, two genera are plotted on the same graph — *Ponera* (left) and *Hypoponera* (right), and *Pogonomyrmex* (left) and *Hylomyrma* (right).

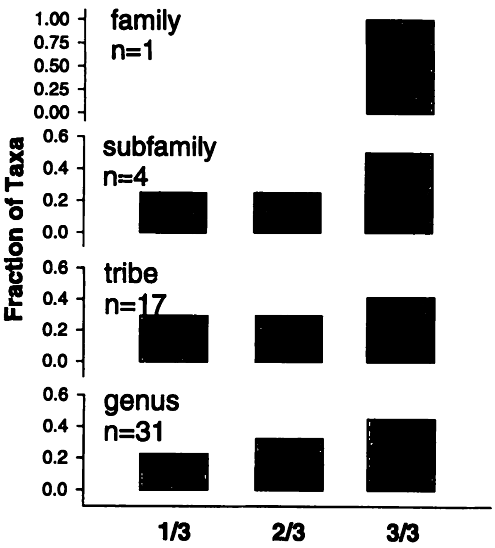

Fig. 4 Location where taxa show their peak abundance, relative to the range of productivities they use (standardized into thirds). If productivity abundance curves were increasing uniformly, maxima would converge in the upper third of the productivity gradient.

0.12 for genera (Pearson's correlation coefficient $r = -0.94$, one-tailed $P = 0.0293$, Fig. 6).

The effects of the two temperature variables showed more variable ant responses. Abundance increased significantly with temperature at the family level and in two of the four subfamilies. For those taxa showing a significant temperature effect, abundance was a positive function of temperature in all but one of the 11 tribes (Formicini) and four of 21 genera (*Formica*, *Myrmica*, *Lasius* and *Tapinoma*). Insolation accounted for about 50% of variation in the abundance of the subfamily Dolichoderinae. Abundance declined with insolation in half the tribes (the forest taxa Dacetini and Stenammini) in which it explained significant variation, and three of seven of the genera.

DISCUSSION

Taxocenes are a common subject of study in ecology, representing, as they do, evolutionarily related sets of species that co-occur in the same habitat. Some attention has been given to the question of intertaxonomic differences in the processes that regulate ecological abundance and diversity (e.g. arthropods vs. vertebrates, Schoener, 1986). This paper makes the case that the choice of taxonomic level, like the choice of spatial and temporal scale (Wiens, 1989; Levin,

Table 4 The range of productivity used by a taxon increases with its taxonomic level (genus, tribe, subfamily). A significant interaction term with abundance (the total number of nests sampled in this study) indicates that the rate that NAP range increases with abundance varies among the three levels of taxonomic resolution. Individual range-abundance curves are listed below. SS = sums of squares, MSE = mean square error, STD = standard deviation, df = degrees of freedom

Source		df	Type III SS	MSE	*F*	*P*
Abundance		1	1844044.1	1844044	20.33	0.0001
Taxon		2	1223646.9	611823.5	6.75	0.0027
Abundance* Taxon		2	1222105.5	611052.7	6.74	0.0027
Error		46	4172326.3	90702.75		
Subfamily	$r^2 = 0.15$					
Intercept		1	1107.01	196.44	5.64	0.0301
Abundance		1	0.17	0.29	0.60	0.6094
Tribe	$r^2 = 0.19$					
Intercept		1	833.84	106.38	7.84	0.0001
Abundance			1.13	0.60	1.894	0.0777
Genus	$r^2 = 0.41$					
Intercept		1	488.77	64.70	7.55	0.0001
Abundance		1	2.85	0.64	4.456	0.0001

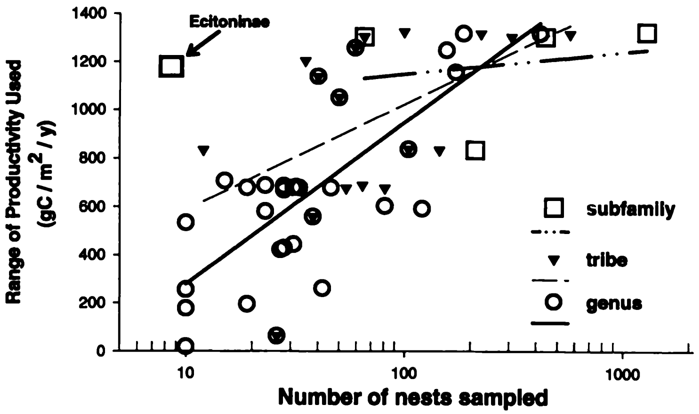

Fig. 5 Range of productivity occupied by subfamilies, tribes and genera represented by 10 or more nests in the dataset. For a given number of nests, higher clades use a broader range of productivity. The Ecitoninae is an uncommon subfamily ($n = 9$ nests found) that did not make the sample size criterion for inclusion. Lines represent best fits from linear regression.

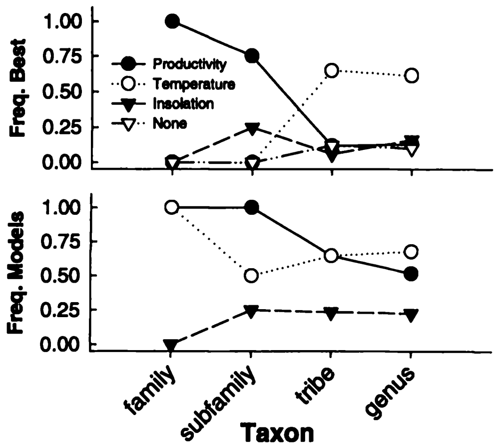

Fig. 6 The results of stepwise regressions (see Table 1) linking abundance to NAP, mean monthly temperature and insolation. Upper graph lists the frequency at which each was the best predictor (i.e. had the highest r^2) across the four taxonomic scales of resolution. Lower graph represents the frequency that each variable explained significant variation in abundance ($P < 0.05$) regardless of its rank in the model. While productivity and temperature both consistently explain variation in abundance, the importance of productivity relative to temperature and insolation declines at smaller taxonomic levels.

1992; Brown, 1995; Maurer, 1999) helps determine the answer to the question, 'What limits a taxocene's abundance?'

Trophic biology and abundance

One factor shaping the abundance of a taxocene is the dietary habits of its species. Tobin's (1994) summary of the trophic habits of ant genera, while the best available, is incomplete. The natural history of most of the ant genera of the world, let alone the species within those genera, is fragmentary and badly in need of more research. The use of bioassays such as isotope analysis (Davidson & Patrell-Kim, 1996) and field cafeteria experiments (Kaspari & Yanoviak, in press) show promising alternative methods toward providing more quantitative estimates of trophic position.

This is the first study, to my knowledge, that examines the trophic structure of taxocenes across the terrestrial productivity gradient. In the ants, herbivores, omnivores and predator taxa show up at approximately one order of magnitude intervals of productivity (1, 9 and 186 gC/m^2/y). This is consistent with hypotheses suggesting that trophic levels should accumulate along productivity gradients (Oksanen *et al.*, 1981).

Furthermore, trophic habits are not distributed randomly across taxa, with consequences for our understanding of taxon distributions at a geographical scale. For example, the rarity of ponerines and the Attinini in low-NAP habitats may arise from their trophic status (as specialist carnivores and detritivores), not their temperature tolerances. To specialize on carnivory or detritivory requires a source of animal flesh and detritus — and a reliable source may only be available in high-NAP environments.

Energy and temperature limitation — the importance of taxonomic level

Little attention has thus far been focused on the sensitivity of ecological pattern to taxonomic level. This analysis suggests that, for the ground ants of the New World, temperature limitation (through convection and insolation) may be the process that best predicts the distribution of genera, while energy limitation best predicts the abundance of ants as a whole. A focus on taxonomic level may be useful for resolving the variation often found in macroecological studies. I give three examples.

Abundance is a key regulator of local diversity (Rosenzweig & Abramsky, 1993; Wright *et al.*, 1993; Kaspari *et al.*, 2000b). If energy limitation increasingly gives way to temperature limitation at finer taxonomic levels, then productivity–diversity curves should also erode. In an exploration of vertebrate diversity patterns, correlations between energy supply and species diversity were weaker and, their signs more variable, at family and genus level than at levels of class and order (Currie, 1991). O'Brien *et al.* (1998), in contrast, analysed the diversity of woody plant species, genera and families in 25 000-km^2 cells across Southern Africa. Diversity at each level was significantly constrained by a combination of moisture and energy availability. However, species richness was more likely to be constrained by low temperatures, while family diversity was more constrained by high temperatures. Taxonomic level can be an important consideration in measuring and interpreting diversity gradients.

Secondly, climate change research has often sought to link species populations to temperature gradients (Steenbergh & Lowe, 1976; Root, 1988b; Parmesan *et al.*, 1999). Such a focus on species trends has thus far limited geographical studies to easily observed and identified organisms such as birds and butterflies. However, this study and others (Clements, 1936; Whittaker, 1956; Holdridge *et al.*, 1971; Stephenson, 1990; Currie, 1991; O'Brien, 1998) suggest that the distribution of plant and animal *taxocenes* is often best predicted by synthetic variables such as NAP that combine gradients of temperature, precipitation and insolation. These synthetic variables are also changing on the global scale. For example, at least two biomes — the northern coniferous forests (Myneni *et al.*, 1997) and tropical rain forests (Phillips & Gentry, 1994) — show evidence of recent increases in NAP (but see Condit, 1997). The present study suggests that the ecological impact of climate change can be explored profitably by surveys of abundance trends in higher taxa that forego species level identification (e.g. curculionid, carabid or scarab beetle taxocenes).

Finally, ants are often suggested to be a thermophilic taxon, given their abundance in deserts, tropical habitats and high insolation sites (Brown, 1973; Hölldobler & Wilson, 1990; Andersen, 1997) — a view codified in Andersen's (1995) climate–taxon classification of ants. The present analysis supports Andersen's schema in two ways. First, it strengthens the inference of thermophily by separating the effects of primary productivity (which increases with temperature in wet habitats) from temperature *per se* (Kaspari *et al.*, 2000a). Secondly, it shows the dominant role that temperature and insolation play at the subfamily, tribe and genus level. Not all ant taxa, as Andersen points out, are thermophilic (e.g. *Tapinoma*, *Myrmica*, *Formica* and *Lasius* increase with decreasing mean temperature of a habitat). However, thermophily is a dominant trend.

Caveats

It is suggested here that newer taxa have smaller ranges because insufficient time has elapsed for species to adapt to and penetrate novel abiotic regimes (see also Janzen, 1967). An alternative scenario is that these taxa have not had time to disperse to habitats in which they would otherwise thrive (i.e. dispersal limitation *sensu strictu*). For example, it is possible that evidence for temperature limitation (e.g. *Trachymyrmex*,

Table 1) reflects insufficient time for the genus to expand beyond the tropics and subtropics (mean temperature and latitude are inversely correlated, Spearman's $r = -0.87$, across the sites studied). While such dispersal limitation cannot be ruled out, most ants have winged reproductive stages, and invasive species such as *Solenopsis wagneri* (formerly *invicta*) have shown the capacity to occupy much of the North American subtropics over the time span of decades (Cokendolpher & Phillips, 1989).

Secondly, this study focuses on ground ant taxocenes. However, in the New World tropics and subtropics, ant assemblages spread into forest canopies (Longino & Colwell, 1997; Tschinkel & Hess, 1999; Kaspari, 2000). Some taxocenes (e.g. the Camponotini and many Dolichoderinae) are thus significantly under-sampled in this study at the high end of the NAP gradient. A quantitative survey of the entire ant fauna of an area — although currently intractable — would probably eliminate the hump-shaped NAP abundance curve for the subfamily Formicinae and give the subfamily Dolichoderinae a bimodal distribution (Fig. 2). This could result in shifts of abundance maxima toward higher NAPs for these subfamilies and, to a lesser extent, for tribes and genera (Fig. 4).

Thirdly, as argued at the outset, abundance $A = B/M$, where M = individual mass and B = biomass. There is evidence that both colony size (Kaspari & Vargo, 1995) and worker size (Cushman *et al.*, 1993) in ants tend to decrease toward the equator. The tropics tend to be warmer and more productive than the temperate zone. If gradients of temperature and/or productivity translate into gradients of colony mass, the mechanisms for some of these patterns would be commensurately complex. This possibility is currently being explored by the author.

Further work is needed to evaluate the ubiquity and nature of the 'taxonomic level' hypothesis as presented here. For example, the hypothesis predicts that at higher taxonomic resolutions (e.g. the Vespoideae for this study), productivity abundance curves should show progressively tighter correlation with NAP, with the effects of abiotic factors playing an increasingly smaller role. Evaluations of other regional ant biotas would test the robustness of this pattern, as would evaluations of other taxocenes (e.g. the North American bird fauna, Robbins *et al.*, 1986; Root, 1988a).

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Appendix 1 Sites used in this study, classified by dominant vegetation. All sites are in the United States and noted with State abbreviation except for tropical forests. LTER = Long-term Experimental Research site, NF = National Forest, SP = State Park, NWR = National Wildlife Refuge, FS = Field Station

Desert shrubland
Deep Canyon Field Station, CA
East Mesa Geothermal Site, CA
Fallon State Park, NV
Jornada LTER, NM
Northern Great Basin Exp. Range, OR
Organ Pipe NM, AZ
Rio Salado, Sevilleta LTER, NM

Tundra
Niwot Ridge LTER, CO

Grassland
Arapaho Prairie, NE
Shortgrass Steppe, LTER
Research Ranch, AZ
Deep Well, Sevilleta LTER, NM
Field Station, Sevilleta LTER, NM
Upper Souris NWR, ND

Woodland/savannah
Cedar Creek LTER, MI
Ordway Prairie, FL
Cold Canyon Preserve, CA
Los Padres NF, CA
Myles Standish SP, MA
Red Tank, Sevilleta LTER, NM
Uinta NF, UT

Coniferous forest
Coconino NF, AZ
Flathead Lake Field Station, MN
Galena Creek SP, NV
Field Station, HJ Andrews LTER, OR
Frizzell Ridge, HJ Andrews LTER, OR
Carpenter Mt, HJ Andrews LTER, OR
Pine Forest, Niwot Ridge LTER, CO
Spruce Forest, Niwot Ridge LTER, CO
Langmuir Observatory, NM
North Temperate Lakes LTER, WI

Temperate deciduous forest
Mark Twain NF, MO
Pioneer Mothers NF, IN
Virginia Coast, LTER, VA

Temperate mixed forest
Bankhead NF, AL
Dykes Gap, Coweeta LTER, GA
Lower Woods, Coweeta LTER, GA
Field Station, Coweeta LTER, GA
Hurricane Gap, Coweeta LTER, GA
Harvard Forest LTER, MA
Torreya SP, FL

Tropical lowland forest
Isla Barro Colorado, Panama
Ft. Sherman, Panama
Las Cruces FS, Costa Rica
La Selva FS, Costa Rica
San Martin, Peru
Yasuni FS, Ecuador

Tropical dry forest
Estacion Chamela, Mexico

Tropical montane forest
Monteverde FS, Costa Rica