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Energy, taxonomic aggregation, and the geography of ant abundance

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Ecological communities and their component populations vary geographically in abundance. Energy theory posits that abundance (the number of individuals area^{-1}) should increase with the ratio of available energy (as net primary productivity, NPP) to individual energy use (i.e. metabolic rate). Most tests of energy theory evaluate the assumption that population abundance decreases as body mass$^{-0.75}$ (a proxy of metabolic rate). Using 664 ant populations from 49 communities we examine how both NPP and body mass – individually and as a ratio – predict abundance (colonies m^{-2}) at these different levels of taxonomic aggregation. Energy theory best predicts ant abundance when populations are aggregated into communities. At the population level, abundance formed a unimodal scatter plot vs all three drivers – colony mass, NPP, and NPP mass$^{-0.75}$ – suggesting that the majority of populations exist below energetic limits set by the ecosystem. At the community level, however, abundance scaled as predicted for mass$^{-0.75}$ and NPP$^{1.0}$, ($b = -0.75$ and 1.0, respectively) and was a positive decelerating function of their ratio (i.e. [NPP mass$^{-0.75}$]$^{0.61}$, $r^2 = 0.68$). Since geographic trends in colony mass and abundance are largely reciprocal – deserts tend to support few large colonies, and tropical rainforests support many small colonies – the geography of ant biomass (g m^{-2}) is remarkably invariant.

Ecologists have long sought to understand how and why abundance (N, the number of individuals of a given taxon in a given area) varies from place to place (Elton 1927). Two sets of theory have been brought to bear on this problem. Demographic theory predicts abundance as a balance of birth, death, and immigration rates (Anderson and May 1979, Hassell et al. 1991, Pulliam and Danielson 1991). While potentially precise and realistic, demographic studies are data-intensive and difficult to implement on more than a handful of species at a time. Energy theory, in contrast, assumes that abundance tracks the available energy in an ecosystem and its use by individuals (Blackburn et al. 1993, Cohen et al. 2003, Brown et al. 2004, Kaspari 2004, Savage et al. 2004). It sacrifices precision for generality using energetic reasoning and allometric empiricism (Yodzis and Innes 1992).

Energy theory builds on two assumptions. It assumes that available energy (measured as net primary productivity, NPP = gC m^{-2} yr^{-1} , the net rate that carbon is fixed by plants and hence becomes available to consumers) sets an upper limit on the number of heterotrophs that an ecosystem can support (Stephens and Krebs 1986, Kaspari 2001). Tests of this assumption at geographical extents are relatively rare. Three have shown decelerating increases in abundance or biomass with NPP (e.g. abundance $\propto$ NPP^b where $b < 1.0$, McNaughton et al. 1989, Moen and Oksanen 1991, Kaspari et al. 2000, Meehan et al. 2004). Energy theory's second assumption is that an individual's energy use is determined by its metabolic rate which in turn increases with body mass (M, Elton 1927, Damuth 1981, Brown and Maurer 1989, Nee et al. 1991, Blackburn and Gaston 1997, White et al. 2007). Since metabolic rate frequently scales as M$^{0.75}$ (Kleiber 1932, Peters 1983) statistical tests often evaluate $N \propto M^{-0.75}$ (see extensive reviews in Blackburn and Gaston 1997, White et al. 2007). The ultimate test of energy theory, thus far confined to a single study of North American birds, revealed that abundance increased with the ratio of productivity and individual metabolic rate, NPP M$^{-0.75}$ (Meehan et al. 2004). Such tests are required to fully vet energy theory, since M can covary with NPP (Kaspari 2005) and, conceivably, populations with similar average M may exist in ecosystems of differing NPP.

Taxonomic aggregation – testing energy theory with populations and communities

Abundance is the number of individuals of a given taxon in a given area (i.e. is the property of a 'taxocene', Hutchinson 1978). Taxonomic scaling adjusts the focus by aggregating populations and forming more inclusive taxocenes (e.g. from summed colonies of the ant *Pheidole multispina,* to summed colonies of the ant genus *Pheidole,* to summed colonies of all ants in the family Formicidae). Tests of energy theory across levels of taxonomic aggregation often give different results. Plots of $N_{population}$ vs $M_{population}$ often resolve (if they do at all) into scatter-plots shaped roughly like right triangles (i.e. populations with the smallest individuals may be rare or abundant; those with the largest individuals in contrast are consistently rare, Blackburn and Gaston 1997, White et al. 2007). Plots of $N_{community}$ vs $M_{community}$ (Li 2002, Meehan et al. 2004) or NPP (Kaspari 2001, Meehan et al. 2004) are less common, but have yielded log-linear relationship more consistent with energy theory.

Taxonomic scaling matters because aggregates can use energy differently than their component populations. This can happen for two reasons. First, aggregates, by representing more of a community's consumers, are more likely to deplete its available energy (Brown and Maurer 1989, Blackburn et al. 1993). This reasoning has generated the dominance hypothesis (Blackburn and Gaston 1997), which posits that the most common species in a community captures a larger share of available energy, is most likely to be energy limited, and thus should parallel the community log–linear relationship (Fig. 1). Second, aggregation also generates taxa of greater phenotypic diversity, often summing across a diversity of trophic levels and abiotic habits (e.g. a community of ants can include fungus cultivators, scavengers, omnivores, granivores, insectivores, and generalized predators, as well as cool and warm temperature specialists, Kaspari 2001). Such niche diversity fosters access to more forms of available energy. If aggregates, but not dominants, track NPP, $M^{-0.75}$, and NPP $M^{-0.75}$, this would support niche diversification as a mechanism driving the pattern.

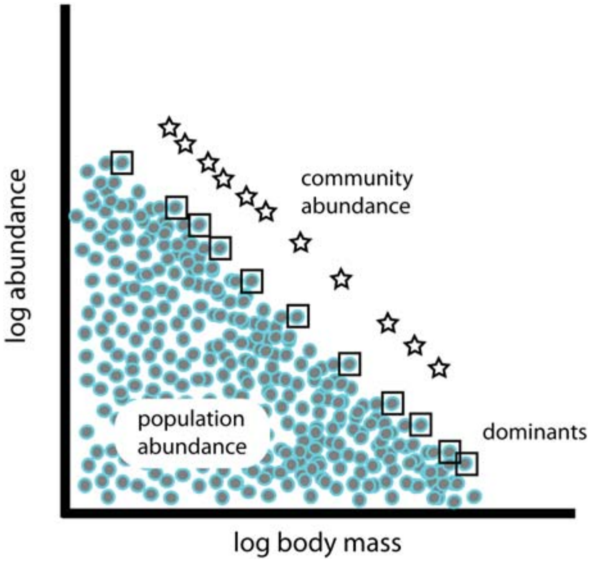

Figure 1. Abundance and body mass should covary in different ways given how organisms and aggregates use energy. Energy theory predicts that community abundance or $N_{community}$ (stars) – the summed abundance of all co-occurring populations – should scale as the average body mass, $M_{community}^{-0.75}$. If population abundances or $N_{population}$ (circles) are frequently held below energetic limits then constraints on individual energy use should generate a triangle scatterplot bounded by $mass^{-0.75}$. The dominance hypothesis predicts that community dominants or $N_{dominant}$ (squares) – the most common population in each community – should parallel the community pattern.

Ants are widespread and ecologically important in most terrestrial ecosystems (Hölldobler and Wilson 1990). Colonies (i.e. the queen(s) and her offspring), like other modular organisms, are genetic individuals (Harper 1981, Hölldobler and Wilson 2008): the colony forages, grows, and reproduces. Measures of ant abundance therefore, to correspond to those for unitary organisms (e.g. birds) must count colonies, and not ants. For this reason (and following Kaspari et al. 2000, Longino et al. 2002, Sanders et al. 2007) we measure N as colonies m^{-2} quantifying abundance quadrats (Agosti et al. 2000). Here we use a unique dataset from 49 ant communities to show that while most ant populations exist at abundances lower than that predicted by energy availability and use, community abundance approaches predictions of energy theory.

Material and methods

From 1994 to 1997, we visited 49 New World sites with a standardized protocol sampling ant diversity, abundance, and colony mass (Kaspari et al. 2000, 2003, Kaspari 2001, 2005). All of our temperate sites were in the northern hemisphere. Sites were sampled during seasons of peak ant foraging (e.g. wet season in a seasonal Panama forest, May in the California chaparral, July in the Colorado tundra).

A site's estimated annual NPP was calculated from evapotranspiration, which in turn was calculated from mean monthly temperature, rainfall, as well as site soil and vegetation (Thornthwaite and Mather 1957, Kaspari et al. 2003). As most localities were at biological field stations, nature preserves, or U.S. Long Term Ecological Research (LTER) sites, these data were readily available from site managers or local airports.

Quantifying abundance

At each locality, we laid out a randomly oriented transect of 30 1 × 1 m plots. Ant colonies were counted in a systematic fashion, collecting litter nests, counting soil nests, then baiting for less conspicuous nests. In forests, most colonies are found in pieces of litter (e.g. twigs, rolled leaves, between leaves, inside pieces of wood). Each piece of litter was inspected over a white tray, and every harvested colony placed in a plastic bag. When the ground was cleared of litter, the soil was scanned for holes and tumulus indicating a nest. These nests were marked with toothpicks, and ants crawling out of them were collected for vouchers. The next day, plots were baited with shortbread cookies (pecan sandies). These cookies, with fats, carbohydrates, and proteins attract all but the most specialized predator ants and revealed more nest entrances. After 30 min, the plots were inspected for ants carrying cookie crumbs into nest entrances. These additional nests were marked with toothpicks, and voucher ants collected. A list of ant species is available from the senior author. Vouchers are in MK's collection at the Univ. of Oklahoma.

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). We thus used a conservative estimate of population abundance ($N_{population}$ = colonies m^{-2}), defined as the number of plots (of 30) in which a nest entrance was observed or a litter nest was collected. Likewise, community abundance ($N_{community}$ = colonies m^{-2}), is defined as the sum total of nests across all populations in each of the 49 communities. To test the dominance hypothesis (Blackburn and Gaston 1997) we used the abundance of the most common population (or, in some cases, populations, $N_{dominant}$) in each of the 49 communities.

Quantifying colony mass and metabolic rate

To establish colony metabolic rate, we first estimated colony mass ($M_{population}$, g dry mass), for each of the 664 populations. This required data on worker number and worker mass. We estimated worker number from harvested reproductive colonies (i.e. those with queens and at least one reproductive pupae or adult). Where nest excavation was impossible, or when the only record was a nest fragment (e.g. workers plus pupae) we used a value for that species from another site or from the literature (Kaspari and Vargo 1995). When no such colony data for that species was available, we used the mean of the $\log_{10}$ worker number for that genus from literature sources (see Kaspari 2005 for further description and links to data). We calculated worker mass from five pinned worker ants from each population using head lengths that were then entered into subfamily specific regressions (Kaspari and Weiser 1999). Log_{10} means of worker mass and number were calculated for each population; the mean mass of a colony in a given population was the product of that population's mean worker mass and number.

Other parts of a colony (such as reproductives) can vary annually and/or with colony size (Tschinkel 1993, Cole and Wiernasz 2000, Kaspari et al. 2001). However we believe worker mass is a good proxy for colony mass as alate biomass scales linearly with worker mass across 15 ant species (Shik 2008) and added variation in mass arising from missed castes would likely be small relative to the 10 000 000-fold range observed with workers alone. Likewise, major workers from dimorphic species, found in only 3 of 82 genera in this study, were not measured given the scarcity of majors in most nest collections.

To test energy theory using $N_{community}$ we calculated the mean colony mass $M_{community}$ across all populations weighted by their local abundance, $N_{population}$. As worker mass and number were log-normally distributed and varied orders of magnitude, simple arithmetic community means would be strongly biased by rare and massive populations. To avoid this bias, we first calculated $\log_{10}$ values for worker mass and number for each population and took a community mean of those log-transformed values.

To quantify an ant colonies' metabolic rate, we rely on recent experiments with whole colonies of *Temnothorax rugatulus* (T. Cao pers. comm.) and *Pogonomyrmex californicus* (Waters et al. 2010) and a review of the existing literature on colony metabolism (Hou et al. 2010) that suggest a metabolism scales as $M^{0.75}$. We estimated the average metabolic rate for an individual in a population as $M_{population}{}^{0.75}$ and that of an average individual in a community as $M_{community}{}^{0.75}$. Jensens inequality (Smallwood 1996) posits $M_{community}{}^{0.75}$ may significantly deviate from the weighted sums of $M_{population}{}^{0.75}$. We thus also calculated this latter estimate of community metabolism as a check on the first.

Statistics

N was distributed differently at population and community levels of aggregation, and we adjusted our statistics appropriately. Plots of $N_{community}$ and $N_{dominant}$ were log-linear and were described with reduced major axis regression using the program RMA (Bohonak 2004), as there was measurement error in both the x and y axes. Confidence intervals were constructed by bootstrapping 500 times with replacement.

Plots of $N_{population}$ were flat-bottomed polygons. We tested for the polygon's predicted log-linear upper bound by 1) binning population data by log10 (for $M_{population}$, and NPP $M_{population}{}^{0.75}$) or 0.5log10 (for NPP), 2) selecting up to 5 populations with the highest $N_{population}$ per bin, and 3) performing OLS linear, quadratic, and cubic regression (the cubic term allowing for a better fit to polygons which are skewed left or right). OLS, not RMA, regressions were used here because the probability that a population is incorrectly binned is lower than the probability it was assigned a precise value of M, NPP, or NPP $M^{-0.75}$. We use the AIC procedure to distinguish which of the 7 possible combinations of variables best described the upper boundary of each polygon (Draper and Smith 1981).

Results

Energy theory and the distribution of 664 $N_{popuiation}$'s

$N_{population}$ formed roughly triangular scatter-plots against NPP, $M_{population}$, and NPP $M_{population}{}^{-0.75}$ (Fig. 2, bottom row). The bottoms were set by our minimum sampling resolution 0.033 colonies m^{-2} (Fig. 2). *Aphaenogaster rudis,* a temperate hardwood forest species of intermediate mass, yielded the highest $N_{population}$ of 0.7 colonies m^{-2} (i.e. 21 of 30 plots occupied).

Contrary to energy theory, populations with the smallest M did not generate the maximum $N_{population}$ (Fig. 2, row 3). The relationship instead was unimodal, best fit by a mixed polynomial model (Table 1) that peaked at ca 0.01 g. Consistent with energy theory, $N_{population}$ increased monotonically with NPP (Fig. 2) but decelerated, reaching a plateau at ca 1000 gC m^{-2} yr^{-1}. When both drivers were combined in the ratio NPP $M_{population}{}^{-0.75}$ (i.e. per-colony energy use) the upper boundary was unimodal (Fig. 2, bottom right).

Energy theory and the distribution of 49 $N_{community}$'s

Unlike $N_{population}$, when populations were aggregated, the resulting $N_{community}$ was a linear function of three variables from energy theory. $N_{community}$ ranged from a low of 0.017 and 0.03 colonies m^{-2} (for the Oregon mountainside and a creosote desert) to a high of 6.5 and 9 colonies m^{-2} in

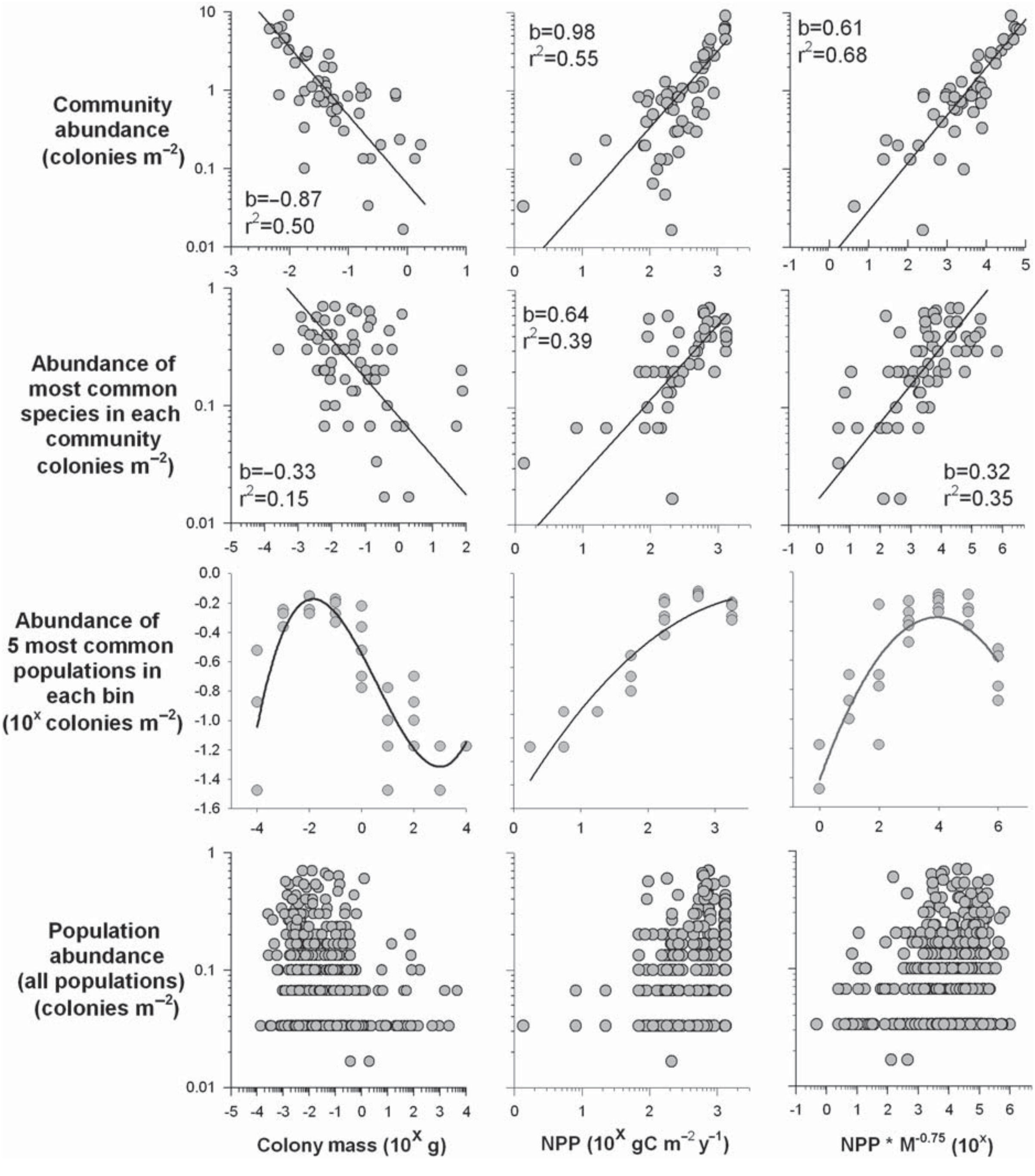

Figure 2. Colony abundance covaries in different ways with three drivers from energy theory – colony mass (M), net aboveground productivity (NPP), and per-colony energy NPP $M^{-0.75}$ – in 49 ant communities. Abundance is analyzed at three levels of aggregation – all species in the community, the numerical dominant(s) of each community, and all 664 populations studied. In the first two rows, lines are fit by RMA regression; b is the exponent and r^2 is the coefficient of determination for the power law arising from this regression. In the third row, lines are best polynomial fits describing the upper boundary in row four.

Panamanian and Ecuadorian rainforests. $N_{community}$ decreased as $M_{community}^{-0.87}$ (Fig. 2, Table 2), consistent with the predicted –0.75, but also not different from –1.0. Likewise, $N_{community}$ increased as $NPP^{0.98}$, indistinguishable from the exponent of 1.0 predicted by energy theory (Table 2). Finally, per colony energy availability scaled as $(NPP\ M_{community}^{0.75})^{0.61}$. This relationship with per-capita energy use accounted for 2/3rds of global variation in community abundance, 24% more variation than NPP (Table 2). The alternate formulation of per colony energy, which calculated average community metabolism as the weighted mean of estimated population metabolisms gave a nearly identical estimated exponent (b = 0.58, standard error 0.0983) to that plotted in Fig. 2.

The dominance hypothesis (Blackburn and Gaston 1997) posits that community abundance curves are log-linear because they are made up disproportionately of populations that capture the most energy in their respective communities.

Table 1. Analysis of the upper boundary of scatterplots relating the abundance of 664 ant populations to three variables from energy theory (Colony mass, NPP, NPP mass$^{-0.75}$) . The AIC procedure is used to distinguish which model, of the 7 possible combinations of variables, best described the upper boundary.

$r^2 = 0.76$	AIC = 108			
Colony mass	Estimate	Error	t value	Pr > |t|
Linear	–0.333	0.038	–8.60	<0.0001
Quadratic	–0.034	0.008	–4.16	0.0002
Cubic	0.020	0.003	5.62	<0.0001
Intercept	0.929	0.056	16.45	<0.0001
$r^2 = 0.86$	AIC = 121			
NPP	Estimate	Error	t value	Pr > |t|
Linear	0.406	0.149	2.72	0.0106
Quadratic	–0.073	0.021	–3.48	0.0015
Intercept	0.501	0.219	2.28	0.0294
$r^2 = 0.80$	AC79			
NPP × $M^{-0.75}$	Estimate	Error	t value	Pr > |t|
Linear	0.664	0.095	6.98	<0.0001
Quadratic	–0.132	0.019	–6.84	<0.0001
Intercept	0.479	0.098	4.85	<0.0001

However, when only $N_{dominant}$s were plotted, these curves diverged from those plotting $N_{community}$s (Fig. 2, row 2, Table 2). $N_{dominant}$ decreased as colony mass$^{-0.33}$ deviating significantly from the predicted –0.75 and accounting for little variance ($r^2 = 0.15$, Fig. 2, Table 2). Likewise, $N_{dominant}$ increased as NPP$^{0.64}$, a rate less than the predicted NPP$^{1.0}$. Finally, $N_{dominant}$ increased as per colony NPP$^{0.32}$, accounting for slightly less variation than NPP alone. In sum, populations of dominant species did not seem to drive community patterns of their respective communities, as predicted by the dominance hypothesis.

Ant biomass across 49 communities

The community biomass of ants ($M_{community} \times N_{community}$) varied 1000-fold across the 49 ecosystems studied here (Fig. 3). Ant biomass was invariant with NPP (RMA regression 95% confidence interval –1.3 –1.7, $r^2 = 0.14$). Low NPP environments like shrub and grasslands spanned the observed range of community biomass. Beyond 600 gC m^{-2} yr^{-1}, ant community biomass varied only ca five-fold.

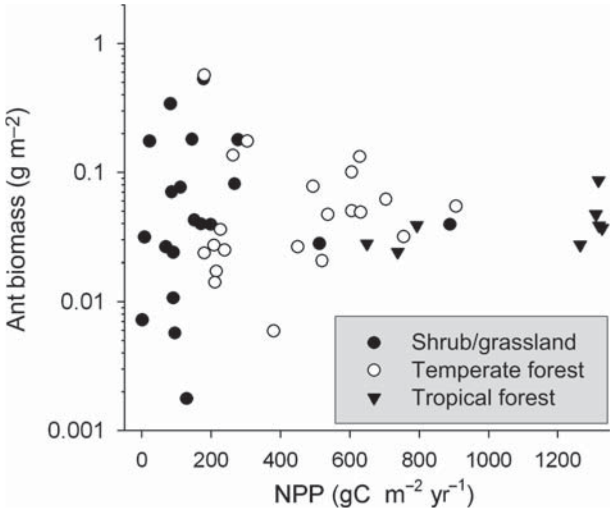

Figure 3. Ant community biomass (summed across all co-occurring populations) across 49 sites arrayed across the terrestrial productivity gradient. Sites are classified by vegetation type.

Discussion

Taxonomic scaling is a useful, if underappreciated analytical tool, allowing the same question to be asked, (in this case, 'What regulates the geography of abundance?') for increasingly inclusive, or aggregated, evolutionary groups (O'Brien et al. 1998, Kaspari 2001, Gotelli 2004). In energy theory, taxonomic aggregation makes a difference. Plots of $N_{population}$ suggest that most ant species are far from their energetic maxima. This is particularly true for species with small colonies in tropical rainforests, the most productive terrestrial ecosystems studied here. However, when populations were aggregated taxonomically as $N_{community}$, (i.e. the taxocene including all of the family Formicidae) abundance decreased with average colony mass$^{-0.87}$ and increased with NPP$^{0.98}$, exponents consistent with the predicted –0.75 and 1.0. Estimates of per-colony energy availability, accounted for 2/3 of the global variation in community abundance, more than NPP or colony mass alone ($r^2 = 0.68$ vs 0.55 and 0.50).

$N_{community}$ – aggregation creates more effective energy harvesters

One hypothesis for why taxonomic aggregation accounts for more variation in abundance – that community abundance is driven by energy-limited numerical dominants (Blackburn

Table 2. Evaluating three models from energy theory – using reduced major axis regression – that predict the abundance of whole ant communities and community dominants only.

N	Energy variable	Lower 95% CI	Intercept	Upper 95% CI	Lower 95% CI	Slope	Upper 95% CI	r^2
Community	M	0.029	0.063	0.125	1.054	0.871	0.690	0.497
	NPP	0.000	0.003	0.012	0.789	0.975	1.446	0.549
	NPP M^{-075}	0.001	0.007	0.018	0.508	0.611	0.769	0.680
Dominant	M	0.044	0.080	0.123	0.467	0.330	0.237	0.146
	NPP	0.001	0.006	0.014	0.495	0.640	0.928	0.393
	NPP M^{-075}	0.006	0.017	0.033	0.250	0.321	0.425	0.350

and Gaston 1997) – received little support in this study. Compared to $N_{communty}$, the abundance of dominants was more poorly predicted by M and NPP, by both r^2 and the match of exponent to theory. This suggests that the act of aggregating rare and common species together is part of the explanation as to why these co-occurring populations are collectively energy limited.

We suggest that sets of species using different fractions of an ecosystem's energy supply collectively deplete that energy more effectively (Dunson and Travis 1991, Kaspari 2001, Cohen et al. 2003). The $N_{population}$ of a species that eats only spider eggs (Brown 1957) or forages only in the subtropical winter (Tschinkel 1987) should by itself poorly track ecosystem NPP. As part of a taxonomic aggregation, however, such populations help harvest and assimilate NPP in its many biotic and abiotic contexts. If true, our 'more and diverse consumers hypothesis' makes a useful prediction: scaling communities to still higher levels of aggregation (in our case, first adding colonies from the Families Vespidae and Scolidae, then all the rest of the Hymenoptera) should track NPP supply even more accurately.

Consistent with energy theory, a per-colony measure of energy performed better than either of its two components, M or NPP. In a similar test using a dataset collected by amateur ornithologists, 23% of the variation in bird abundance across North America was accounted for by per-bird energy use (Meehan et al. 2004). Our study, using a more standardized survey that benefitted from the fact that ant colonies can be counted with quadrats, accounted for 68% of the geographical variation in ant abundance. Both studies conclude that $N_{community}$ scales to per-capita $\text{energy}^{0.61}$. We know of no comparable datasets on the geography of animal abundance.

$N_{population}$ – are tiny colonies in productive habitats invisible or rare?

Rank abundance curves consistently show that communities are constructed of a few dominant and many rare populations (Rosenzweig 1995, Hubbell 2001). As long as rare species are not also large-bodied, rank abundance curves are prima facie evidence against uniform energy limitation among a community's populations. The scatter-plots at the bottom of Fig. 2 further support this conclusion.

A secondary prediction from energy theory is that the upper boundary of abundance–energy plots, describing the most common species per unit body mass or NPP, should scale as $M_{population}^{-0.75}$ and $NPP^{1.0}$. Instead, the upper boundary of the abundance–mass curve was unimodal (Fig. 2, bottom left). It increased from 10^{-4} to 10^{-2} g, and then decreased up to 10^4 g. The ant species with the smallest colony mass – typically litter nesters with 10–100 tiny workers – do not appear to exist at proportionately higher abundances. This may be an artifact of detectability (Blackburn et al. 1993): the increase phase may be due solely to our inability to find the smallest colonies. Let us assume the size of this bias is the sole explanation for unimodality (and that the energetic hypothesis is otherwise correct). One can do this by extrapolating, right to left, on the portion of the graph where abundance increases as colony mass decreases. If so, the smallest colonies on our 1-m^2 plots would have to be roughly 200–300 fold more undetectable than colonies of the median mass. While we cannot falsify this hypothesis, we suspect bias alone cannot account for the unimodality, as we used a variety of methods, and spent up to 5 h harvesting, colonies from a single quadrat.

A similar unimodal boundary has been documented for species populations of North American birds (Brown and Maurer 1987). Brown and Maurer speculated that the high-energy demands of the smallest, nectarivorous birds limited them to rare, high-energy patches. This seems unlikely for the ectotherms studied here. The tiniest ant taxa in the increase phase include a variety of trophic habits: predators (*Pheidole ruida, Ponera pennsylvanica*), herbivores (*Brachymyrmex* C1), and brood parasites (3 species of *Solenopsis* subgenus *Diplorhoptrum).* As colony mass increases, these common species give way to generalists from the genus *Paratrechina* and *Aphaenogaster,* with the two largest colony mass bins representing 'superorganisms' like the leafcutter *Atta mexicana,* and the army ants *Labidus coecus* and *L. spinidosis* (Hölldobler and Wilson 1990). We conclude that in ants, massive colonies may be limited to common (plants) or energy rich (prey) food items, but small colony size allows for a variety of trophic habits. The reason for the relative rarity of small-colony species remains a puzzle.

Climate, energy, and metabolism in ecological communities

While there has been much interest in the relationship between abundance and body size (see Blackburn and Gaston 1997, White et al. 2007 for summaries) and the geography of body size (Blackburn et al. 1999, Smith et al. 2004) there has been little work linking the two. Considerable opportunity remains for a synthesis given that the two driving variables in energy theory – NPP and metabolic rates – arise in multiple, nonlinear ways from temperature and precipitation. For example, individual metabolic rate is often a positive decelerating function of body mass (as $M^{0.75}$) and positive accelerating function of body temperature (T, as $e^{1/T}$, Gillooly et al. 2001). However the adult body mass of ectotherms is frequently smaller when they are raised in warmer environments (Atkinson and Sibly 1997). Similarly, NPP is co-limited by solar energy and precipitation (whichever is in shortest supply, Rosenzweig 1995), suggesting another positive or neutral role for temperature in regulating abundance. Insofar as energetic approaches to abundance are useful, climate should have a large, complex role to play as a template.

We finish with one surprising result from this study: our failure to find an increase in ant community biomass over the 1000-fold gradient in terrestrial NPP. At <200 gC m^{-2} yr^{-1} (mostly desert scrub and grasslands) community biomass varied widely. This large variance was likely an artifact: the 1000-fold fewer colonies in low NPP ecosystems resulted in enhanced sampling error of both $N_{population}$ and $M_{population}$. Above 600 gC m^{-2} yr^{-1}, however, biomass was fairly constant at 0.05 g ants dry weight m^{-2}. Biomass is a product of individual mass and abundance. Beyond an NPP of 100 gC m^{-2} y^{-1}, average colony size in ant communities tends to decrease as NPP$^{-1.0}$ (Kaspari 2005) even as, shown here, summed abundance scales as NPP$^{1.0}$ (see also Sanders et al. 2007). Furthermore, the average size of an ant worker in a community decreases with temperature$^{-0.03}$ (Kaspari 2005). Gradients of mass and abundance, both tracking temperature and to some extent rainfall (Kaspari 2005) appear to cancel each other out. As a consequence, tropical everwarm forests support larger numbers of (on average) smaller colonies of (on average) smaller ants than their temperate zone counterparts. Small colonies have a shorter lifespan and proportionately higher metabolic rate (Hou et al. 2010). It thus appears that as one moves up the NPP gradient, ant communities are capturing and turning over energy at an increasingly rapid rate.

The gradients in body size, abundance, and biomass we document here for ants clearly do not hold for terrestrial plants communities (Whittaker 1970) and we know of no comparable data for terrestrial consumers. However, the prevalence of Bergmann's rule in ectotherms population (Atkinson and Sibly 1997) suggests that community biomass need not increase lockstep with ecosystem productivity. Invertebrates, particularly soil taxa that can be sampled with quadrats, provide ample opportunity for understanding the geography of life history and community structure.

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