

Three energy variables predict ant abundance at a geographical scale

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Energy theory posits three processes that link local abundance of ectotherms to geographical gradients in temperature. A survey of 49 New World habitats found a two order of magnitude span in the abundance (nests m⁻²) of ground nesting ants (Formicidae). Abundance increased with net primary productivity ($r^2 = 0.55$), a measure of the baseline supply of harvestable energy. Abundance further increased with mean temperature ($r^2 = 0.056$), a constraint on foraging activity for this thermophilic taxon. Finally, for a given mean temperature, ants were more abundant in seasonal sites with longer, colder winters ($r^2 = 0.082$) that help ectotherm taxa sequester harvested energy in non-productive months. All three variables are currently changing on a global scale. All should be useful in predicting biotic responses to climate change.

Keywords: abundance; temperature; energy theory; ants; ectotherms; climate change

1. INTRODUCTION

Abiotic conditions have long been known to shape the abundance of populations within local habitats (e.g. Andrewartha & Birch 1954; Whittaker 1956). Community ecology builds from these studies, often focusing on taxocenes—assemblages that share a common ancestor (Hutchinson 1978). A key goal is to learn how taxocene properties like abundance, morphology, and diversity, vary across abiotic gradients in time and space.

Ants are ubiquitous, ecologically important and relatively easy to sample (Hölldobler & Wilson 1990). They are thus models for the development of taxocene ecology (Andersen 1997). Here we propose three processes that link temperature to ant abundance and analyse their effects with a survey of 49 New World ant assemblages.

2. ENERGY THEORY AND ECOLOGICAL ABUNDANCE: THREE PROCESSES

Energy theory assumes a consumer taxon's abundance arises from its ability to capture and sequester a habitat's harvestable energy (Connell & Orias 1964; Odum 1971; Wright *et al.* 1993; Kaspari *et al.* 2000). It models a taxocene as a chemostat—with energy flowing in and out, and the amount of energy within the chemostat at any one time representing the taxocene's biomass, or standing crop. A taxocene's biomass, divided among individuals of a given body size, generates its abundance. Energy theory posits that consumer abundance changes with the rate at which energy enters the habitat, the fraction of that energy accessible to the taxocene, and how quickly, once harvested, the energy is lost again through the combined processes of metabolic heat, excreta and death. Each of these processes is subject to temperature.

(a) Productivity hypothesis

Net primary productivity (NPP, gC m⁻² yr⁻¹) measures the rate at which carbon is fixed by plants minus carbon

lost through plant respiration. NPP is thus one measure of the rate at which energy is made available to a habitat's consumers. Terrestrial NPP is co-limited by rainfall and solar radiation (Rosenzweig 1968; Lieth 1975) and has been used to predict the diversity of species in a variety of taxocenes (Rosenzweig & Abramsky 1993). Energy theory explicitly assumes that the habitat's energy supply sets an upper limit to a taxocene's abundance (Wright *et al.* 1993; Srivastava & Lawton 1998; Kaspari *et al.* 2000). If taxocene abundance is determined solely by NPP, then productivity and abundance should be positively correlated.

(b) Thermal limitation hypothesis

Abiotic factors (or 'conditions'; Begon *et al.* 1996) further regulate abundance by regulating access to a site's primary productivity. Every physiological function is sensitive to temperature to some degree. Foraging activity tends to occur within a predictable range of temperature for a given taxon (Precht *et al.* 1973). For ants, the foraging activity of an 'average' species ($n = 41$; Hölldobler *et al.* 1990) peaks at 32.3 °C (s.d. = 11.2) and ceases at 40.6 °C (s.d. = 10.4). Both the tendency to forage at warm temperatures and the abundance of ants in warm deserts has prompted a number of authors to suggest that ants are a thermophilic taxon (Brown 1973; Hölldobler *et al.* 1990; Andersen 1997). Soil nests provide thermal refugia in the hottest environments, allowing a colony to harvest warm habitats and retreat to the cool of the nest in the heat of the day (Harkness & Wehner 1977; Tschinkel 1987).

If mean annual temperature limits the ability to harvest and assimilate productivity, then for a given NPP-increasing temperatures should increase ant abundance. However, as NPP is often temperature limited in mesic sites (Lieth 1975), a positive correlation between temperature and abundance might arise as an artefact of an NPP-abundance relationship. The statistical separation of these two effects is thus essential.

(c) Metabolic cost hypothesis

The basal metabolic rate describes the minimum rate that harvested energy is returned to the environment. In endotherms, basal metabolic rates are 'U-shaped' functions of temperature—organisms devote more energy to thermoregulation when their environment is cold and when it is hot (Precht *et al.* 1973). Ectotherms, in contrast, have basal metabolic rates that are a generally positive function of temperature (Schmidt-Nielsen 1990). In a number of ant species, metabolic rate in the laboratory is a positive, decelerating function of temperature over ranges of 0–35 °C (Nielsen *et al.* 1999; Vogt 1999).

These three factors (NPP, foraging efficiency, and basal metabolic rate) can be incorporated into a single energy balance equation for a taxon:

$$dE/dt = NPP \times f - c,$$

where E is energy, f is foraging efficiency (unitless, varying from 0 to 1) and c are the basal metabolic costs (in $\text{gC m}^{-2} \text{yr}^{-1}$). The first term describes the rate at which energy is harvested and the second term describes the rate at which that energy is lost. Energy theory suggests that the balance between energy intake and loss sets an upper limit to a taxon's abundance in a habitat. However, if foraging rate and metabolic costs both increase with temperature, this sets up a conflict for ectotherms striving to harvest the maximum amount of energy while sequestering that energy against metabolic loss.

We propose that habitats with seasonal temperature cycles allow ectotherms to minimize this conflict. Picture two habitats with the same NPP and mean monthly temperature but differing in the seasonality of temperature. In the aseasonal habitat, production is spread thinly over the 12 months, and the taxon accrues the same metabolic costs all year round. In a habitat with seasonal variation in temperature, primary production is concentrated in the warm summer months near the peak of a taxon's foraging efficiency. Foraging intake, a product of NPP and efficiency, is thus maximized when NPP is seasonally pulsed. Winters with temperatures near 0 °C, in contrast, lessen metabolic heat loss at the same time that plant productivity is at a seasonal low (Lieth 1975; Tauber *et al.* 1986). Seasonal environments thus enhance a taxon's ability to harvest energy in the summer, and enhance energy conservation in the winter by lowering metabolic costs when NPP is at its minimum. The benefit of seasonal cold would be especially high for organisms like the ants, with high maximum foraging efficiencies at the expense of high basal metabolic rates (Oster & Wilson 1978; Peters 1983; Nielsen 1986).

Although we are unaware of any tests of this hypothesis, ants have been shown to exploit the relationship between temperature and metabolic costs. Numerous studies have shown soil nesting ants daily moving pupae vertically in soil nests so as to keep pupae at the optimum temperature for growth (see Hölldobler & Wilson 1990). In laboratory experiments on a temperature gradient, *Solenopsis invicta* moved developing pupae to colder parts of the nest when food was scarce (conserving energy), and to warmer parts of the nest when food was abundant (maximizing growth; Porter & Tschinkel 1993). Furthermore, an ant colony can minimize the colony's risk of

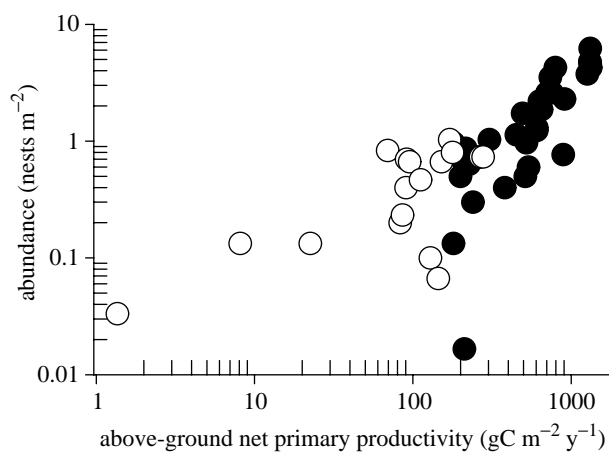


Figure 1. Ant colony abundance increases with aboveground net primary productivity across 49 sites. Open circles, tundra, scrub and grassland habitats; filled circles, forested habitats.

death by freezing. In sub-zero conditions workers form a ball with the queen at its centre providing a layer of sterile tissue that intercepts lethal ice crystals (Heinze & Hölldobler 1994).

Here we report the results of a survey of New World ant assemblages. We test the above hypotheses' predictions that ant abundance

- (i) will be highest in more productive habitats;
- (ii) for a given productivity, will be highest in warm habitats;
- (iii) for a given productivity and temperature, will be highest in habitats with more months with an average temperature below 0 °C.

3. MATERIAL AND METHODS

We studied 49 ground ant assemblages from 1994–1997, including two from South America, six from Central America, and 41 from North America (see Appendix A). Mean monthly temperature and rainfall were gathered from stations on site or in nearby cities and airports (Anonymous 1995). We estimated a site's primary productivity by first calculating its actual evapotranspiration (Thornthwaite & Mather 1957). Actual evapotranspiration was related to aboveground NPP using a polynomial equation ($r^2 = 0.93$, Rosenzweig 1968; Kaspari *et al.* 2000). Sites ranged in estimated NPP from 1 to 1315 $\text{gC m}^{-2} \text{yr}^{-1}$.

At each site, we used a standard protocol to estimate ground ant abundance. Thirty 1-m² 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 a thorough search of each plot, aided by baits. Abundance (ant nests m⁻²) was estimated from the counts of nests on the 30 1-m² 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.

NPP was uncorrelated with the other two abiotic variables of the energy hypothesis: mean monthly temperature ($r = 0.18$, $p = 0.23$) and months below 0 °C ($r = -0.09$, $p = 0.53$). These two abiotic variables were negatively correlated ($r = -0.75$, $p < 0.0001$). Ant abundance (nests m⁻²) was regressed against primary

Table 1. Three-way regression of \log_{10} ant colony abundance against three variables from energy theory

variable	d.f.	estimate	s.e.	T for parameter = 0	p	partial r^2
intercept	1	-2.52	0.245	-10.331	0.0001	—
\log_{10} NPP	1	0.679	0.082	8.317	0.0001	0.564
mean temperature	1	0.045	0.010	4.544	0.0001	0.056
months < 0°C	1	0.126	0.036	3.501	0.0011	0.082

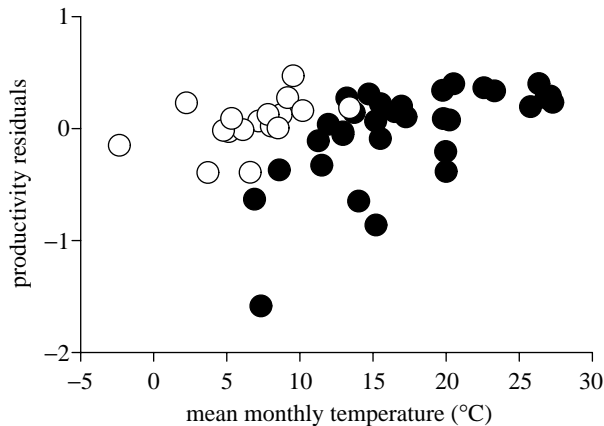


Figure 2. The residuals of figure 1 plotted against a site's mean temperature. Filled circles indicate aseasonal sites (no months in which mean monthly temperature was less than 0°C) and open circles indicate seasonal sites (one or more months at less than 0°C).

productivity (both \log_{10} transformed), mean temperature, and number of months with a mean monthly temperature of less than 0°C.

4. RESULTS

Over the 49 sites, NPP and ground ant abundance varied over three and two orders of magnitude, respectively. The productivity hypothesis predicts a positive correlation between NPP and abundance. NPP alone accounted for 56% of the variation in ant abundance (figure 1; $F_{1,48} = 60.67$, $p = 0.0001$, ant abundance = $0.0123 \text{ NPP}^{0.738}$). The exponent was significantly less than 1 (H_0 , slope = 1, $F_{1,47} = 7.59$, $p < 0.0083$) and thus represents a positive, decelerating curve.

To evaluate the thermal limitation and metabolic cost hypotheses, we used a three-way regression, with NPP, mean temperature, and months with less than 0°C added sequentially (table 1). After NPP was accounted for, these variables explained an additional 5.6% (mean temperature) and 8.2% (months < 0°C) of variation in ant abundance (model $F_{3,46} = 38.26$, $p < 0.0001$). We examined the shapes of these relationships by plotting the mean temperature against the productivity-abundance residuals (figure 2), and months with less than 0°C against the productivity-temperature residuals (figure 3). The temperature-abundance relationship, though significant, showed considerable scatter, resolving itself into seasonal (months < 0°C) and aseasonal (no months < 0°C) sites. This pattern remained when mean

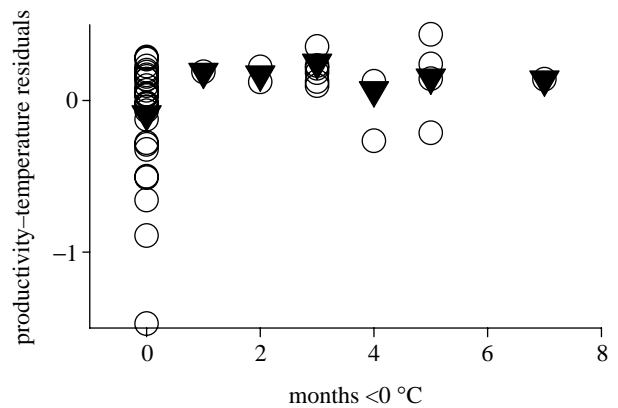


Figure 3. The residuals of figure 2 plotted against the number of months a site's average temperature was less than 0°C. Triangles show arithmetic means for each category.

temperature effects were removed (figure 3). To assure that these results were robust to normality assumptions, we checked figures 2 and 3 with non-parametric correlations: both the temperature effect (Spearman's $r = 0.48$) and months with less than 0°C effect (Spearman's $r = 0.39$) were significantly positive ($p < 0.01$).

5. DISCUSSION

This study is the first we know of that explores factors regulating the abundance of a taxon over the terrestrial productivity gradient. Seventy per cent of the variation in ant abundance was accounted for by three variables that delimit an ectotherm taxon's ability to capture available energy and sequester it against metabolic loss. Ectotherms represent most of the world's animal biomass and biodiversity (Wilson 1993). Understanding the mechanisms that regulate ectotherm abundance is key to predicting the impacts of climate change.

Abundance was a positive decelerating function of NPP, which accounted for half its variation. This suggests two things of interest. First, energy supply sets an upper limit to abundance in ant taxocenes. Second, the curve's deceleration suggests that energy limitation is more profound at lower NPPs. One potential bias is that we did not sample the tropical canopy. Herbivores consume between 11 and 14% of leaf production in tropical forests (Coley & Barone 1996) and ants commonly nest in the canopy in the subtropics and tropics (Majer 1976; Tschinkel & Hess 1999) where they are missed by our sampling protocol. Both factors, by underestimating abundance and overestimating NPP at high-NPP sites,

would cause an apparent deceleration in the NPP–abundance curve. However, the curve decelerates before there is a canopy fauna (the non-forest portion of the curve has an exponent less than 1; $1.061 \times \text{NPP}^{0.599}$, $r^2 = 0.56$, $n = 17$, $p < 0.0005$; figure 1). This deceleration deserves further attention and may result from increased competition from other herbivores (McNaughton *et al.* 1989) or fire (Wedin 1995), decreases in average colony size toward the tropics (Kaspari & Vargo 1995), or some other factor(s).

Beyond the upper limit to ant abundance set by NPP, an additional 13.8% of variation in abundance is accounted for by temperature and its seasonality. Ants are frequently classified as thermophilic (e.g. Brown 1973), a classification strengthened here by separating out the effects of NPP, which is also often temperature limited (Rosenzweig 1968). Furthermore, this study suggests that seasonality, instead of raising metabolic costs (Connell & Orias 1964) may benefit ectotherms that use winters as metabolic refugia. How common is this pattern? For other ectotherms to flourish in seasonally cold environments they must be able to (i) reduce winter metabolic costs and mortality, and (ii) locate and harvest summer resources that are patchy in time. Ectotherms with high metabolic costs and foraging speeds (social insects, facultative endotherms) may best be able to exploit environments

with seasonal pulses of resources and intervening cold spells. In contrast, endotherms that lack torpor and annual ectotherms that overwinter as eggs should not benefit from cold winters in this way. Finally, habitats with long winters support no more colonies than those with a single month of winter (figure 3). The costs of prolonged winters (e.g. risk of frost mortality; Heinze & Hölldobler 1994) may outweigh the benefits of energy conservation. Studies of other taxocenes will help resolve these issues.

Climate change studies by zoologists have thus far emphasized population responses to temperature gradients (e.g. Root 1988; Parmesan *et al.* 1999). Taxocenes too, deserve attention, with NPP possibly acting as the key environmental gradient. For example, in northern coniferous forests both NPP and growing season appear to be increasing (Myneni *et al.* 1997). This study suggests differing responses between taxa that do and do not use winter as a metabolic refuge.

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APPENDIX A

The sites used in this study as classified by dominant vegetation. All sites are in the USA and noted with state abbreviations except for tropical forests. An annotated site list is available from the author. LTER, long-term experimental research site; NF, national forest; SP, state park; NWR, national wildlife refuge; FS, field station.

dominant vegetation	site
desert shrubland	Deep Canyon Field Station, CA; East Mesa Geothermal Site, CA; Fallon State Park, NV; Jornada LTER, NM; Northern Great Basin Experimental Range, OR; Organ Pipe NM, AZ; Rio Salado, Sevilleta LTER, NM
tundra	Niwot Ridge LTER, CO
grassland	Arapaho Prairie, NE; Shortgrass Steppe LTER, CO; Research Ranch, AZ; Deep Well, Sevilleta LTER, NM; field station, Sevilleta LTER, NM; Upper Souris NWR, ND
woodland and/or savannah	Cedar Creek LTER, MI; Ordway Prairie, FL; Cold Canyon Preserve, 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 Mountain, 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; Fort 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

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