

A test of species–energy theory: patch occupancy and colony size in tropical rainforest litter-nesting ants

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Species–energy theory can account for spatial variation in the abundance and community composition of animals, though the mechanisms of species–energy theory are under contention. We evaluated three competing mechanisms at the local spatial scale by conducting an *in vivo* light manipulation over supplemental ant nests placed in the leaf litter of a Costa Rican tropical rainforest. We found that the light environment did not alter the 10% rate of occupation of the supplemental nests, but light did alter the size of colonies and the genus-level composition of the community. Light levels in the foraging range were positively associated with colony sizes of all ants, whereas light levels directly on the nest site were predictive of the occurrence of ant genera. Colonies of specialized predators, dacetine ants, were larger in more shaded foraging environments, and the functional group of generalized myrmicines exhibited an opposite pattern, with smaller-sized colonies in response to shading. Responses of twig-dwelling ants to the light environment were most consistent with the metabolic cost hypothesis as a mechanism of species–energy theory. We found mixed support for the thermal energy availability hypothesis, and scant support for the chemical energy hypothesis, as the litter depth, a measure of prey density, was not predictive of ant responses. In summary, at the local scale, we found patterns in colony size and life history are governed by light-dependent mechanisms.

Along latitudinal and elevational gradients, the community structure of animals varies predictably with temperature, as do life histories (Andersen 1997, Gotelli and Ellison 2002, Sanders 2002, Sanders et al. 2003). The mechanisms accounting for these patterns, all involving energy-driven constraints, remain unclear and under contention (Kaspari et al. 2000a, Dunn et al. 2009, McGlynn et al. 2010a, Adler et al. 2011). Manipulative experiments to evaluate how energy and temperature affect animals should be used to test competing mechanisms (Wiens 1989, Dunn et al. 2009), as observations of animal densities and ambient light do not necessarily predict preferential habitat (McGlynn et al. 2010b). *In situ* manipulations of microclimate at the spatial scale of single organisms may be used to infer differential responses among taxa to thermal conditions. In turn, these findings may be used to develop and evaluate hypotheses about how animals and their communities respond to spatial variation in climate. Here we describe a study in which we manipulate the light environment of litter-dwelling ants to test hypotheses regarding the responses to altered thermal regimes.

Sanders et al. (2007) suggested that local patterns in ant communities reflect differences in resource abundance, whereas temperature regulates patterns at larger scales. This notion tacitly assumes that fine-scale differences in

microclimate do not necessarily structure ant communities at the local scale. This suggestion was essentially presented as a challenge to ant community ecologists, which has not yet been subjected to adequate scrutiny. To our knowledge, there have been no published field experiments manipulating temperature to evaluate the effect on ant colony sizes, and little is known about community responses to temperature manipulations (but see Lessard et al. 2009).

In the case of ants under the canopy of forests, the amount of light radiating a nest is a major predictor of nest temperature (Smallwood 1982, Bristow et al. 1992). The light transmitted through the canopy into the colony's foraging range predicts the temperature experienced by ants that have left the nest searching for food (Kursar and Coley 1992, Kaspari 1993). By manipulating light conditions above ant nests and in the foraging area of their colonies, we may learn how co-occurring taxa differentially respond to microclimate, in terms of patch occupancy and colony ontogeny. We expect heterogeneous responses, reflecting preferences of colonies in the laboratory (Mezger and Pfeiffer 2010).

There is a well-supported large-scale trend for decreasing colony sizes corresponding to increases in mean temperature (Jeanne 1979, Kaspari and Vargo 1995). An application of these continental-scale patterns, to predict local-scale

patterns, would lead to the prediction that microclimates with more light (and hence higher temperatures) will contain smaller colony sizes. This is opposite of the prediction of energy-based theories, in which more microclimates with greater transmission of light in forest understories should be favored nesting sites for their increased productivity and thermal properties (Perfecto and Vandermeer 1996).

In the understory of tropical rainforests, the dim light that passes through the canopy creates sunflecks, generating ephemeral high temperatures that are highly localized. Among plants, the photon flux and temperature of sunflecks stimulates growth and reproduction, and variability in plant responses to sunfleck availability is a major predictor of community assembly (Chazdon and Pearcy 1991). Equivalent mechanisms may account for some of the considerable heterogeneity in litter-nesting ant communities in tropical rainforests (Kaspari 1996). According to the species energy theories applied to ants (Kaspari et al. 2000b) these more productive sun patches and sun flecks with higher photon flux density would provide more resources for ants.

Three competing mechanisms of species–energy theory, as formalized by Kaspari et al. (2000b) generate different predictions regarding the responses of animals to manipulations of light conditions. The ‘thermal energy availability hypothesis’ posits that the density and community composition of ectothermic animals is shaped by their access to thermal energy. According to this hypothesis, the community composition and life histories of animals should differentially respond to light conditions in the foraging area of a colony, reflecting access to energy while seeking resources for the colony. In contrast, the ‘metabolic cost hypothesis’ emphasizes that the metabolic demands of ectotherms may vary with the relative cost of maintenance and growth. Under this hypothesis, higher light at nesting sites will facilitate greater metabolic rates, with concomitant larger colonies. Conversely, shaded colonies with lower basal metabolic needs and less efficient foraging would result in smaller colonies. The distinction between these two hypotheses is the scale of light transmission: the thermal energy availability hypothesis predicts differences based on the foraging conditions of the colonies, whereas the latter predicts differences based on the microclimate of the nesting site of colonies.

The chemical energy hypothesis proposes that organisms are constrained not by their access to energy via temperature, but by the energy bound in food consumed by ectotherms. According to this hypothesis, the localized abundance of resources should be the best predictor of species occurrences and life histories, and that ambient differences in light affect

ant colonies insofar as they alter the availability of basal resources, such as leaf litter. While energy limitation is predictive of community composition and animal life histories, disentangling these three competing hypotheses is challenging, as the thermal conditions of the nest and the thermal conditions of the foraging range often are tightly linked – or at least not readily manipulated – in most experimental systems.

In this paper, we describe a field experiment under the canopy of a tropical rainforest in which we have manipulated the light environment for litter-nesting ants and have provided supplemental nests. This approach will enable us to evaluate animal responses to altered thermal regimes, in terms of community composition and colony size. These responses will be applied to evaluate contrasting predictions of different mechanisms energy-based theories (Table 1).

Material and methods

The study was conducted January–July 2009 at La Selva Biological Station (10°26′N, 83°59′W), Sarapiquí Canton, Heredia Province on the Caribbean slope of Costa Rica. La Selva is located in a lowland tropical wet forest, with an average annual rainfall of 4 m (McDade and Hartshorn 1994). Among five sites, 247 pairs of plots were created representing conditions varying in light and forest age. With reference to the La Selva trail system, these sites included the Camino Experimental Sur, Sendero Surá, Camino Circular Cercano, Camino Circular Lejano and Sendero Jaguar. All pairs of plots were placed at least 10 m apart from another, allowing for full independence of foraging ranges of litter-nesting ant colonies. In each pair of plots, a shade treatment plot and a control plot were established 30 cm apart. In the shade treatment, a 30 × 30 cm piece of mesh was above the litter and anchored by wire flags that held the mesh ca 10 cm above the litter layer. Litter was placed on top of the mesh to provide additional shade, however rainfall continued to pass through the apparatus readily. Supplemental nests (bamboo twigs) were placed on top of the litter, and under the shade of the mesh, providing a potential nesting site for colonies of litter-dwelling ants. In the control treatment, a twig of equivalent proportions was also placed on top of the litter, without the presence of the shade provided by the mesh. After four weeks, the twigs were removed from all the sites and examined for ant nests. All ants were identified to species or morphospecies using the resources available at <www.evergreen.edu/ants>. Colony sizes were evaluated

Table 1. A comparison of predictions associated with hypothesized mechanisms of species–energy theory. Underlined items were supported by the results.

Hypothesis	Predicted response of ants to supplemental nests		
	Presence of ants	Colony sizes of ants	Functional group frequencies
Thermal energy availability	positively associated with canopy cover	negatively associated with canopy cover; no effect of treatment	vary with canopy cover
Metabolic cost	less frequent in shade treatment	<u>positively associated with light at nests; smaller in shade treatments; response may vary with functional group</u>	vary with light at nests; differ between treatment and control
Chemical energy	positively associated with litter depth	positively associated with litter depth; no effect of treatment	varies with litter depth

by counting the number of adults inside each nest. Analyses were conducted at the genus level, on account of the high species richness of the site. Species were assigned to one of four functional groups reflecting both taxonomy and diet (Andersen 1995, 1997, McGlynn 2006, McGlynn et al. 2009). These groups were: dacetines (a tribe of mesofaunal predatory specialists: *Pyramica*, *Strumigenys* and *Acanthognathus*); generalized myrmicines (subfamily members that recruit to and defend resources without maintaining territories: *Pheidole* and *Solenopsis*); opportunists (non-aggressive species that invest into rapid resource discovery: *Paratrechina*) and poneromorphs (predaceous ants with a similar morphology: *Hypoponera*).

In each plot, mean litter depth was calculated using a standardized approach, using a wire flag inserted into the litter (Kaspari 1996, McGlynn et al. 2009). Depth was measured at five points per plot (at each corner of the plot and in the center). Light transmitted directly on the nest site was estimated simultaneously using a standardized diazo paper apparatus method on a single day to estimate peak photon flux density, PPF (Friend 1961, Bardon et al. 1995). This method provided results that are highly correlated ($r^2 > 0.90$) with direct measurement of PPF, and enabled simultaneous measurement PPF for direct comparisons among plots. One apparatus was placed at each plot where an ant nest was found. Light was measured in the foraging range of the colonies occupying the nest sites, outside the shade apparatus, using a spherical densitometer, calculating the mean value from values measured at the cardinal directions. In prior studies on the surface of leaf litter, it has been found that light is highly predictive of temperature and humidity at the spatial scale of the present experiment (Matlack 1993).

All statistical analyses were conducted using JMP 9 or JMP 10 (SAS Inst., Inc.). We used a t-test to compare PPF between shade and control treatments, and used linear regression to evaluate the relationship between canopy cover and PPF between treatment and control. To test the predictions of species–energy theory mechanisms, we used generalized linear models (GLM) to evaluate how shade treatment, light, litter depth and forest type influenced ant inhabitants of the plots, following the guidelines of Bolker et al. (2009). To evaluate the occupancy of nests (the presence/absence of ants in supplemental nests), we used a binomial distribution logit link function GLM, in which $P(x) = 1$ in cases where no colony was present. We used a normal distribution GLM to evaluate the relative effects of functional group, shade treatment, peak PPF and canopy cover on colony size (log transformed for normality). The occurrences of colonies in each functional group were evaluated using a logistic regression with shade treatment, canopy cover, PPF and litter depth predictor variables.

Results

The shade treatments resulted in lower PPF relative to the control (mean exposure_{control} = 3.89 (SD 1.06); mean exposure_{treatment} = 1.19 (SD 1.23); $t_{90} = 11.43$; $p < 0.00001$). Moreover, the shade treatments decoupled the relationship

Table 2. Generalized linear model for parameters predicting the presence or absence of ants in supplemental nests. There were no significant factors (whole model $\chi^2_4 = 4.39$, $p = 0.36$).

	Parameter estimate	χ^2	p
Intercept	-0.11	0.002	0.97
Shade treatment	[control] 0.32	0.81	0.37
Canopy cover	0.01	0.21	0.64
Light at nest (PPF)	-0.20	1.04	0.30
Mean litter depth	-0.18	2.55	0.11

between canopy cover and peak PPF (control: $F_{1,25} = 14.32$, $p = 0.0005$, peak PPF = 9.42–0.064 canopy cover; $r^2 = 0.24$; shade: $F_{1,45} = 2.11$, $p = 0.15$, peak PPF = 3.95–0.032 canopy cover; $r^2 = 0.04$).

Nests remained in the field at 247 plots for four weeks. Among the 494 nests, 47 (9.5%) were inhabited by ant colonies containing queens, with 24 in the control plots and 23 in the treatment plots. Overall, the occupancy of nests was independent of treatment, canopy cover, PPF, and litter depth (Table 2).

The GLM for colony size indicated an effect of the shade treatment and PPF, as well as differential responses by different functional groups of ants (Table 3, Fig. 1). As the relationship between colony size and canopy cover was marginally insignificant in the GLM, we conducted a linear regression to visualize the relationship (Fig. 2). The GLM testing for the factors predicting the occurrence of a functional group in each site were not affected by treatment, canopy cover, PPF or litter depth ($\chi^2_{12} = 7.18$, $p = 0.85$).

Discussion

As temperature variation coincides with latitudinal and elevational biodiversity gradients (Kaspari and Vargo 1995, Sanders 2002), we sought to manipulate light conditions at the local scale to evaluate whether large-scale patterns in ant communities are recapitulated in the fine-scale biology of ant communities. We found that the difference in colony sizes are explained by light levels that occur directly at nest sites. Whereas the amount of light that passes through the canopy onto the ground is associated with the colony sizes of ants, in an experimental manipulation we found that the light at the nest itself is the prevailing factor accounting for variation in colony size.

Table 3. Generalized linear model for parameters predicting colony size among 47 colonies in experimentally placed supplemental twigs. The whole model was well supported ($\chi^2_7 = 20.66$, $p = 0.004$). The dependent variable was log transformed for the normal distribution fit of the GLM. *indicates significant factors.

	Parameter estimate	χ^2	p
Intercept	4.79	4.60	0.031
*Shade treatment [control]	-0.64	4.84	0.028
Canopy cover	-0.04	3.69	0.055
*Light at nest (PPF)	0.35	5.28	0.022
Mean litter depth	-0.18	3.05	0.081
*Functional group [dacetine]	0.66	5.59	0.018
Functional group [generalized myrmicine]	-0.07	0.04	0.830
Functional group [opportunist]	0.37	1.44	0.23

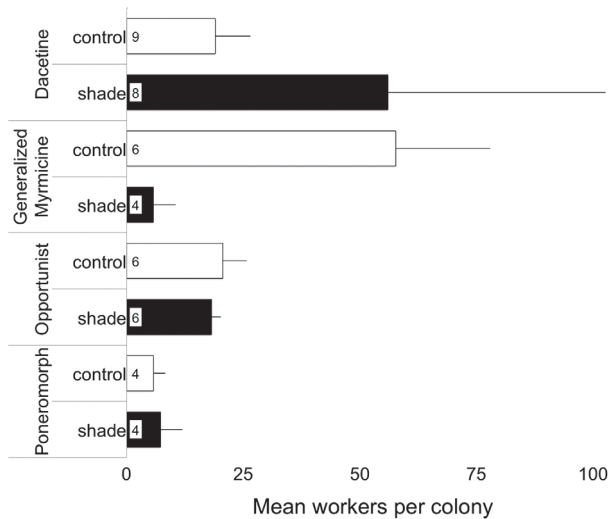


Figure 1. Colony sizes of ant functional groups in control and shade treatment plots. Closed bars indicate colony sizes in experimentally shaded plots and open bars indicate colony sizes in control plots. Errors bars indicate SE; value labels indicate n. Statistics are presented in Table 3.

Based on the predictions of the species–energy theory hypotheses, we find that the metabolic cost hypothesis accounts for variation in colony size (Fig. 2). The potential differences among taxa in their functional response to treatment may reflect differences in brood temperature requirements (Mezger and Pfeiffer 2010) or competitive strategies (Cerda et al. 1997). In the Generalized Myrmicine functional group, warmer patches were occupied by large colonies, and we observed in *Solenopsis* that foundress queens with very small colonies occupied spaces underneath experimental shade. This local result is commensurate with the geographic distribution of *Solenopsis*, with a predilection for direct sunlight and higher temperatures (Perfecto and Vandermeer 1996, Tschinkel 2006). In contrast, the dacetine genera had larger colonies in more

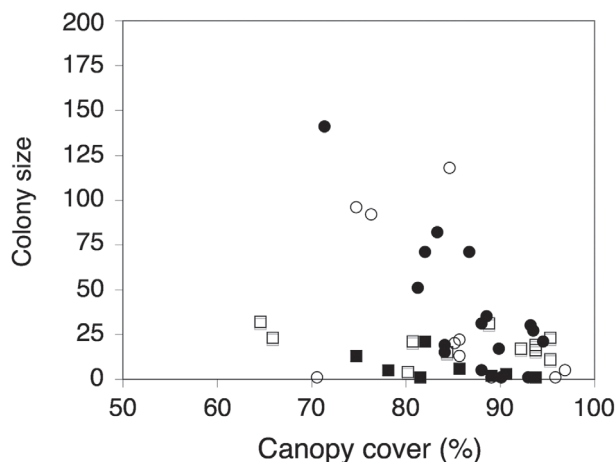


Figure 2. Colony sizes relative to canopy cover. Open circles indicate dacetines; closed circles, generalized myrmicines; open squares, opportunists; closed squares, poneromorphs. For all colonies pooled, colony size = 149.1–1.43 canopy cover, $r^2 = 0.136$, $F_{1,48} = 7.55$, $p = 0.008$.

shaded areas. This observation is consistent with field observations of ant behavior, as dacetine ants of the tropics move with a slow tempo reminiscent of a sloth. It would be expected that these ants, with presumably slower metabolisms, seek out nests in the shade, which would result in lower metabolic costs. Another potential explanation is that the larger colonies are more likely to occupy a more shaded microclimate that may increase the density of their collembolan prey, however Lessard et al. (2011), working in a temperate North American forest, did not find that collembolan densities responded to larger shade treatments.

Our results reinforce the recent suggestion that light may be the most critical variable in locally structuring forest ant communities (Mezger and Pfeiffer 2010). To date, investigations have consistently found that the amount of leaf litter, as a correlate of prey availability and as potential habitat, is the greatest predictor of occurrence and colony size on the local scale (Kaspari 1996, McGlynn 2006, McGlynn et al. 2009). These prior findings would imply support for the chemical energy hypothesis, however, prior investigations did not manipulate light levels, which otherwise would be unaccountably heterogeneous.

The species-rich assemblage of tropical litter-dwelling ants continues to puzzle ecologists using niche-based models to evaluate community structure. In this forest cohabit more than a hundred litter dwelling species which appear to overlap very closely in nearly all dimensions of niche space that one can think to measure, save thermal preferences (Mezger and Pfeiffer 2010); this is analogous to the pattern found in canopy trees of rainforests. Tropical ecologists have long looked toward the physiological responses to light limitation as a mechanistic explanation for the complexities of species richness and community assembly among the plants that grow to constitute the canopies of rainforests (Ricklefs 1977). The ant communities on the forest floor experience the same thermal environment as seedlings competing for the light required to survive and grow up to the canopy. Our findings suggest that animal ecologists, especially those studying ectotherms such as ants, may look towards the thermal biology of light flecks transmitted through the canopy to understand local patterns in life histories and community structure.

Acknowledgements – This project was supported by Tropical Ecology Mentorship Program (NSF OISE-0854259 and OISE-1130156), the CSUDH LS-AMP program (NSF HRD-0802628), and the OTS NSF-REU program. Sean Menke provided helpful comments on the manuscript. We thank student research volunteers and the staff of La Selva Biological Station for assistance.

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