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Species energy and Thermal Performance Theory predict 20-yr changes in ant community abundance and richness

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Abstract. In an era of rapid climate change, and with it concern over insect declines, we used two theories to predict 20-yr changes in 34 North American ant communities. The ecosystems, from deserts to hardwood forests, were first surveyed in the 1990s. When resurveyed in 2016–2017, they averaged 1°C warmer with $200 \text{ g C-m}^{-2} \cdot \text{yr}^{-1}$ higher plant productivity. Ant colony abundance changed from -49% to +61%. Consistent with Thermal Performance Theory, colony abundance increased with temperature increases $< 1^\circ\text{C}$, then decreased as a site's mean monthly temperature change increased up to $+2.4^\circ\text{C}$. Consistent with Species Energy Theory, (1) ant abundance tracked changes in a measure of energy availability (net above-ground productivity, $\text{g C-m}^{-2} \cdot \text{yr}^{-1}$) and (2) increases in colony abundance drove increases in local plot- and transect-level species richness but not that of Chao 2, an estimate of the size of the species pool. Even after accounting for these drivers, local species richness was still higher ~20 yr after the original surveys, likely due to the increased activity of ant workers. These results suggest community changes are predictable using theory from geographical ecology, and that warming can first enhance but may ultimately decrease the abundance of this important insect taxon.

Key words: ants; global change; insects; net primary productivity; species energy theory; temperature; thermal performance theory.

INTRODUCTION

The abundance and species richness of ecological communities, co-occurring species of a given taxon, covary in time and space. A key task of ecology is to quantify and predict changes in community abundance and richness in response to anthropogenic increases in temperatures, species invasions, eutrophication, and habitat destruction (Vitousek 1994). There is mixed but growing evidence for declines in insect abundance and richness especially in heavily modified landscapes (e.g., Hallmann et al. 2017, reviewed in Leather 2018). However, given the challenges in interpreting meta-analyses after the fact (Gonzalez et al. 2016), there remains a need for hypothesis-driven, standardized data on community trajectories (Cardinale et al. 2018) especially for

invertebrates (McGill et al. 2015). Two bodies of theory can prove useful in predicting such changes in abundance and species richness.

Species Energy Theory (Wright 1983) posits that net primary production (NPP, the rate that plants fix carbon and make it available to consumers) constrains a consumer clade's community abundance (the total number of individuals from that clade per unit area). It also posits that increases in community abundance can enhance local richness since (1) a larger local assemblage of colonies can "sample" more species from the regional species pool and/or (2) increases in average population size can decrease the per-species probability of extirpation (Kaspari et al. 2003). Thus, Species Energy Theory predicts that increases in NPP should increase consumer abundance and, in turn, local species richness.

Thermal Performance Theory (Kingsolver and Huey 2008, Angilletta 2009) posits unimodal, left-skewed, thermal performance curves (TPCs): an ectotherm's physiological performance accelerates with temperature

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to a maximum beyond which lies a quick descent in physiological performance ending in the ectotherm's death. The result of a given increase in environmental temperature on a population's fitness thus depends on its TPC and the range of temperatures it experiences (Sunday et al. 2011). In Thermal Performance Theory, a small increase in temperature stands a better chance on average of increasing an ectotherm's survival, growth, and reproduction; a large increase risks pushing the population beyond its TPC's maximum, rapidly reducing its growth and survival. At the community level, Thermal Performance Theory sums over the dynamics of its constituent populations, predicting that as temperatures increase, community abundance should also increase before eventually crashing. Moreover, populations/communities from temperature-variable environments are predicted to be better adapted to, and less prone to suffer from, a given increase in temperature, *ceteris paribus* (Angilletta 2009).

Species Energy and Thermal Performance Theory thus have considerable promise for predicting changes in ectotherm communities when temperature and productivity vary. Consistent with Species Energy Theory, net aboveground productivity (NAP, the NPP occurring aboveground) accounted for 55% of the thousand-fold variation in colony abundance across 49 ant communities (Kaspari et al. 2000), with abundance constraining diversity more at progressively smaller spatial grains (Kaspari et al. 2003). Consistent with Thermal Performance Theory, small temperature increases can increase butterfly populations (Warren et al. 2001). Few data bear, however, on the prediction of an acceleration in abundance with rising temperature. The most suggestive comes from a comparison of warming chambers that increased temperatures 1.5°–5.5°C over ambient in a cool and warm forest; consistent with acceleration, the activity-abundance of ants only increased in the warmer forest (Stubble et al. 2013).

Ants are a thermophilic taxon with thermal maxima that regularly exceed 50°C (Diamond et al. 2012, Kaspari et al. 2015). Ant abundance and diversity varies broadly across Earth's surface (Weiser et al. 2010, Gibb et al. 2017). Ant populations (Chew and De Vita 1980, Porter and Jorgenson 1988, Brown et al. 1997) and communities (Horvitz and Schemske 1990, Resasco et al. 2014, Donoso 2017) often show dramatic changes in abundance and composition at annual to decadal time scales, attributed variously to periodic disturbances (e.g., El Niño, as proposed by Brown et al. 1997), warming (Pelini et al. 2014), and habitat change (Resasco et al. 2014).

Here, we test predictions from Species Energy and Thermal Performance Theory using a resurvey of 34 North American communities in 2016 and 2017 originally surveyed from 1994 to 1997 (Kaspari et al. 2003). We evaluate key predictions from Species Energy Theory on the nature of community change: that warmer and more productive environments support more ant

colonies and more ant species especially at smaller spatial scales. We do the same for Thermal Performance Theory testing for nonlinear changes in abundance; first increasing then decreasing as the magnitude of an ecosystem's heating increases.

MATERIALS AND METHODS

In 2016 and 2017, we resampled, using identical methods, 34 ant communities across North America first sampled in 1994–1997 (see Kaspari et al. 2003, Appendix S1: Table S1, Fig S1 for maps and methodology). Colony abundance was defined as the total number of colonies found on the 30: 1-m² plots of a sample transect. We measured species richness at three spatial grains: the average number of species (nests and strays) recorded in a 1-m² plot (S_{plot}); the number of species recorded on a transect (S_{transect}), and $S_{\text{Chao 2}}$ (Chao 1984) the richness at a still larger, but unspecified, spatial grain that estimates the size of the species pool sampled by S_{plot} and S_{transect} .

We measured mean monthly temperature, its annual range (average difference in maximum and minimum mean monthly temperature since 1980), and net primary productivity (NPP, g C-m⁻²·yr⁻¹) for each site from existing databases (see Appendix S1), with NPP calculated from actual evapotranspiration (AET) via a modified version of Rosenzweig's (1968) regression that converted annualized AET into measures of aboveground productivity.

Statistics

To test both Species Energy and Thermal Performance Theory, we evaluated how linear, quadratic, and cubic changes in a site's mean temperature, changes in NAP, and its average thermal range accounted for variation in changes in abundance recorded at each site (Data S1: Kaspari_Ants_20yearchange.R). Next we evaluated all possible models with these five variables using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson 2002). AIC_c values for all models using the *dredge* argument were calculated with the *MuMin* package (Bartoń 2018) in R version 3.5.3 (R Core Team 2019). All models having $\Delta\text{AIC}_c < 2$ are considered equally parsimonious (Burnham and Anderson 2002) and are reported. Finally, we used the *lm* argument to evaluate how changes in abundance drove changes in richness, calculated from all ants and just from recorded nests, at three grains: 1-m², transect, and Chao2.

RESULTS

The 34 North American ecosystems were, on average, warmer and more productive ~20 yr after the first surveys in the 1990s (Appendix S1: Fig. S2). All but two sites recorded higher mean monthly temperatures

(range: -0.4°C in a New Mexico high desert to $+2.4^{\circ}\text{C}$ in a central hardwood forest) averaging a 1°C increase (Wilcoxon signed rank test $P < 0.0001$). For estimates of net aboveground productivity, 10 of 34 sites recorded decreases after 20 yr (range: $-206 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for an Arizona high desert to $+876 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for a northern grassland) for an average increase of $205 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Wilcoxon $P < 0.0003$). Changes in the two drivers were weakly, positively correlated (Appendix S1: Fig. S2). Mean monthly temperature range varied from 17°C in a subtropical savannah to 33°C in a northern prairie.

North American colony abundance per 30 m^2 in 2016/2017 varied nearly 100-fold (from 4 colonies at three sites to 99 in a North Carolina hardwood forest). Thirteen of 34 communities registered decreases in abundance (range: -52 nests in an Alabama mixed forest to $+61$ in a North Carolina mixed hardwood forest). There was no consistent trend for a change in abundance after ~ 20 yr (Wilcoxon signed rank test $P = 0.41$).

Thermal Performance Theory predicts abundance will increase and then decrease as temperature change increases. Species Energy Theory predicts abundance will track increases in NAP. Three models were within the criteria of $\Delta\text{AIC}_c < 2$ (Fig. 1, Table 1). All three revealed a nonlinear effect of temperature. Sites with changes in temperature between -0.4° to 1°C showed, on average, 7 more nests per 30-m^2 transect; nest density then decreased, on average, as temperatures increased $> 1^{\circ}\text{C}$. ΔNAP significantly and positively contributed to two of the three best models for abundance. Thus, consistent with Species Energy Theory, for a given change in temperature, communities with increased productivity increased in nest density.

Species Energy Theory predicts that increases in abundance should drive increases in richness at smaller spatial grains (Appendix S1: Fig. S3). At the 1-m^2 plot scale, S_{plot} , ant species richness averaged 3.3 species/m^2 (range: 0.6 in a mixed hardwood forest to 6.4 in a warm desert) with an average 20-yr increase of 0.5 species/m^2

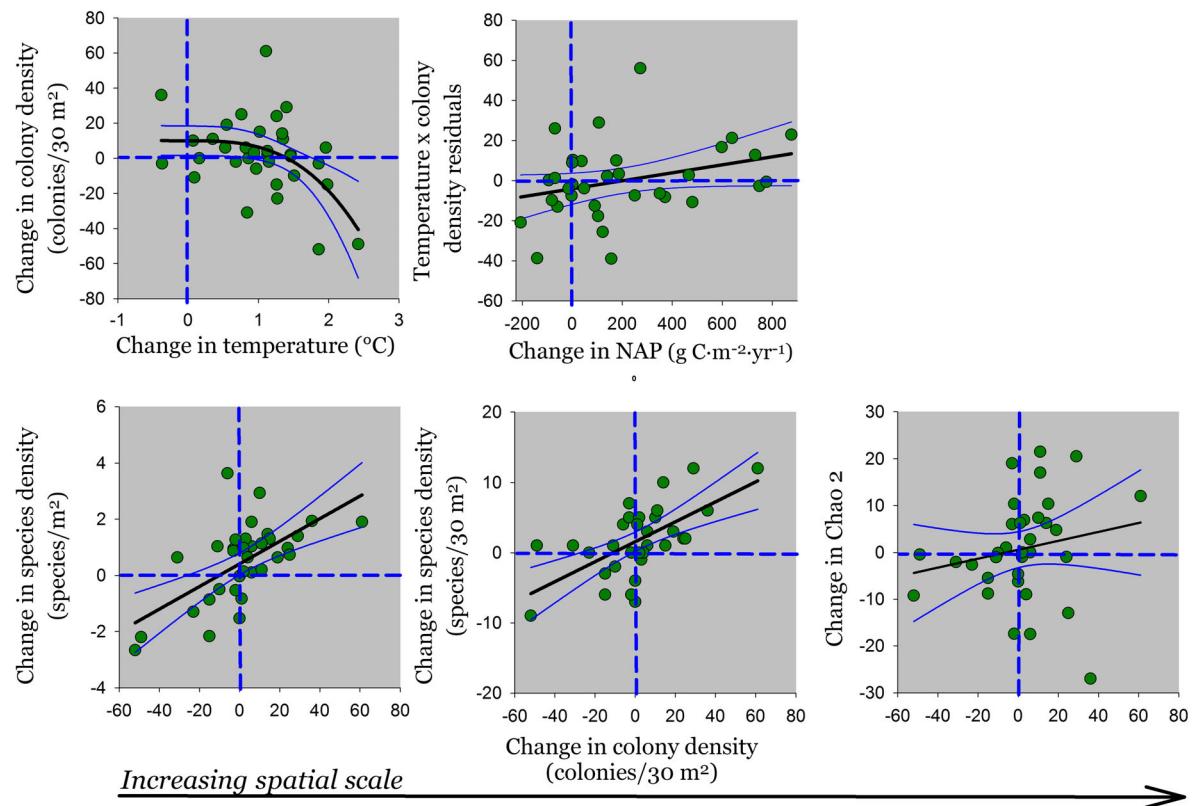


FIG. 1. Consistent with Thermal Performance and Species Energy theory, (top left) ant community abundance increases then decreases as the magnitude of temperature change grows and (top right) for a given rise in temperature, abundance changes are enhanced in high productivity environments. Consistent with Species Energy Theory, increases in abundance drive increases in species richness at small, but not large spatial scales. Species richness at the 1-m^2 plot grain (bottom left), and across the 330-m transect of 30-m^2 plots (bottom middle), increases or decreases in proportion to increases and decreases in abundance across the 34 ant communities. At the largest, spatially ambiguous scale of Chao 2 (bottom right), estimating the number of species in the species pool, abundance effects disappear. Best fit linear regressions, with 95% confidence intervals, are shown. NAP, net aboveground productivity.

TABLE 1. The three best models ($\Delta\text{AIC}_c < 2$) for changes in nest abundance, $\Delta\text{Colonies}/30\text{ m}^2$, all have nonlinear temperature terms as predicted by Thermal Performance Theory.

Intercept	Pr($> t $)	ΔTemp^3	Pr($> t $)	ΔTemp^2	Pr($> t $)	NAP	Pr($> t $)	df	AICc	adj r^2
7.00	0.106	-4.34×10^{-6}	0.001			0.0226	0.058	4	300.4	0.29
10.27	0.038			-9.611×10^{-4}	0.001	0.0260	0.039	4	301.3	0.27
9.92	0.022	-3.57×10^{-6}	0.003					3	301.9	0.22

Notes: Two models show Species Energy Theory's prediction of increasing abundance with productivity. Temp, mean monthly temperature ($^{\circ}\text{C}$); NAP, net aboveground productivity ($\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$); ΔAIC_c , the change in the Akaike information criterion corrected for sample size. Mean monthly temperature range never met criteria for inclusion.

TABLE 2. Tests of Species Energy Theory's "more individuals hypothesis" at three spatial grains.

Δ Species richness	Intercept	SE	Pr($> t $)	$\Delta\text{Colonies}/30\text{ m}^2$	SE	Pr($> t $)	adj r^2
ΔS_{plot}	0.408	0.193	0.042	0.040	0.009	0.001	0.37
$\Delta S_{\text{transect}}$	1.560	0.678	0.028	0.142	0.032	0.001	0.37
ΔS_{Chao2}	0.559	1.885	0.769	0.095	0.088	0.285	0.01
ΔS_{plot} (nests only)	0.076	0.044	0.093	0.026	0.002	0.001	0.82
$\Delta S_{\text{transect}}$ (nests only)	0.456	0.573	0.432	0.119	0.027	0.001	0.37
ΔS_{Chao2} (nests only)	1.597	1.807	0.383	0.228	0.084	0.011	0.16

Note: Top half of the table reports richness for all species found on plots, both colonies and strays. Bottom half reports richness for species recorded on plots as colonies (nests only).

(Wilcoxon signed rank test $P = 0.037$). Across the 30-m² plots of the sample transect, S_{transect} , ant richness averaged 15.7 species/30 m² (range: 1 in an alpine tundra to 29 in a warm desert) with an average 20-yr increase of 1.8 species across the 34 sites (Wilcoxon signed rank test $P = 0.04$). At the largest, but spatially ambiguous, grain described by S_{Chao2} , sites averaged 21 species (range: 1 in the alpine tundra to 42 in the warm desert) with no systematic 20-yr change across the 34 communities (+0.73 on average, signed rank test $P = 0.68$).

Consistent with Species Energy Theory, average species per square meter increased by one species for every 25 colonies added to the transect; average transect diversity increased by one species for every seven colonies added (Table 2, Fig. 1). Moreover, significant intercepts suggest that the 2016–2017 resamples had 0.4 more species per square meter and 1.6 more species per transect over and above those changes driven by increases in abundance. At the largest grain, an estimate of the species pool ΔS_{Chao2} , changes in nest abundance had no effect on changes in richness. When these analyses were repeated using species richness only from recorded colonies, the residual enhancement of species richness (i.e., non-zero intercepts) disappeared (Table 2, Appendix S1: Fig. S4).

DISCUSSION

A resampling of 34 North American ant communities revealed systematic changes, but no evidence for uniform declines, in ant community abundance and species richness after ~20 yr. About one-third of that community

change can be accounted for by applying Thermal Performance and Species Energy Theory, with temperature and plant productivity change as its drivers. Combined, these data suggest that community trajectories in a warming environment are in part predictable.

Perhaps our most novel result is the nonlinear response of ant community abundance to warming. Estimating changes in abundance (i.e., individuals/unit area) is challenging but key to understanding both the biotic impacts of warming on ecosystem processes as well as the origins of diversity gradients (McGill et al. 2015). Thermal Performance Theory, scaling individual performance to population densities, predicts that ectotherm abundance should increase and accelerate, then crash, with rising temperatures. Our cubic regression is consistent with declines in abundance beyond ~1.0°C. A similar decline in ant richness was found in a southeastern North American forest, while a nearby small-scale warming experiment had no effect (Resasco et al. 2014). Our failure to detect an accelerating increase in abundance before the decline may have resulted from the confounding effect of productivity changes, poorly correlated with those of temperature, that also drove changes in ant abundance. Temperature range, in contrast, did not influence abundance dynamics.

We found no uniform decline, but instead often modest increases in colony ant abundance across North America. Another intensive study of protected fields and meadows yielded no 20-yr net decline in the abundance of insect pollinators (Herrera 2018). This contrasts with some recent reports of community insect declines (e.g., Hallmann et al. 2017). One key difference was our

selection of large protected areas; declines are frequently recorded near urban or agro-ecosystems (see review in Leather 2018). Theory and sampling programs that integrate the effects of land use are thus likely vital to understanding patterns of insect community change (Vitousek 1994).

The functional traits of a taxon should also govern their response to environmental change. In this regard, it is hard to imagine an insect that may be more resistant and resilient to modest warming than the ants. Ants are thermophiles, with thermal maxima typically exceeding 40°C (Diamond et al. 2012, Kaspari et al. 2015). Most species can retreat to thermally buffered nests. Like the mobile, generalist butterfly populations that are most likely to increase as temperatures rise (Warren et al. 2001), ants as a clade are dominated by generalized feeders (Clay et al. 2017) with a winged reproductive stage and a simple life cycle (Boulay et al. 2010) less prone to phenological mismatch with host plant species (Parmesan 2006). Finally, ant colonies are also important scavengers (Griffiths et al. 2018); it is possible that ant communities, at least in the short term, benefit from the stress and mortality inflicted by climate change on more susceptible insect populations. If ants are an ectotherm clade likely to benefit from modest increases in temperatures, we predict that, within these communities, omnivorous/scavenging populations, and those that nest in the soil, will be more likely to increase at the expense of specialized predators and those that nest in the less microclimatically buffered leaf litter.

The assumption that abundance constrains richness (Kaspari et al. 2003) is often implicit in studies of anthropogenic change in ecological communities, but rarely explicitly tested (McGill et al. 2015, Cardinale et al. 2018). We document and validate the role of changes in abundance, which accounts for about one-third of the variation in richness changes, as a mechanism linking diversity to climate change. Large-scale, Chao2 diversity changes (resulting from, for example, changes in species ranges, Warren et al. 2018), however, showed no such pattern. This supports the working hypothesis that higher local abundance allowed ant communities to sample more species from the surrounding landscape.

However, we also find local diversity marginally enhanced after ~20 yr beyond that predicted by changes in abundance. One mechanism may lie in the thermal ecology of ectotherm movement: ant worker velocity increases with temperature (Hurlbert et al. 2008, Prather et al. 2018), and more active ants may be more likely to wander into sample plots (see also Gibb et al. 2019). This hypothesis gains support by the disappearance of this diversity enhancement when strays are excluded from diversity measures (Appendix S1: Fig. S4). Moreover, ants, and many other insects, have an effective mobile dispersal phase (Boulay et al. 2010); anything that enhances movement could thus result in higher propagule rain of novel species over more area. This relaxation of dispersal limitation at small spatial scales

can experimentally enhance local richness in grasslands (Tilman 1997) and has recently been found in both agricultural and montane plant communities (Alignier 2018, Steinbauer et al. 2018).

Our results point to the importance of nonlinear changes in ectotherm abundance with global heating: ant abundance increased with warming, but only up to a point. Diversity then tracked abundance at local spatial grains. But it is important to note that we tested community theory with two snapshots separated in time, not by annual sampling (e.g., Warren et al. 2001, Steinbauer et al. 2018, Gibb et al. 2019). As a consequence, we cannot distinguish long-term, inertial changes in ant communities from those that arise and could reverse on an annual time scale. Put another way, we have no data on the resilience of these communities to ecological change. There is some reason to believe that ant communities are resilient. After an El Niño year in a Panama forest, Wheeler and Levings (1988) found that ant declines were quickly erased when temperature and rainfall regressed to the mean. Likewise, an experimental removal of a common Mediterranean ant was erased in 1 yr by the immigration of winged queens (Boulay et al. 2010). Future progress toward understanding the mechanisms underlying changing insect communities requires better data on key drivers (e.g., surface and soil temperatures) and annual, global surveys of the communities themselves (e.g., NEON; Schimel 2011).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2888/suppinfo>

DATA AVAILABILITY

Data are available from the Open Science Framework repository: <https://doi.org/10.17605/osf.io/rc6wq>