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On the geography of activity: productivity but not temperature constrains discovery rates by ectotherm consumers

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Abstract. Consumer activity—the rate that individuals move through and discover items in their environment—can constrain population interactions and ecosystem services. We introduce a model that assumes consumer activity is co-limited by the abundance and velocity of consumers, which in turn are constrained by two global drivers: net primary productivity (NPP) and environmental temperature, respectively. We test it with data from a recent study showing how arthropod activity decreases with latitude and elevation. The maximum discovery rates (discoveries per day) of these ectotherms increased linearly with NPP and accounted for the observed latitudinal gradient in activity. The mean temperature of the warmest month in contrast had no consistent effect on activity. An ecosystem's NPP, which provides carbon to build individuals and sugars to fuel them, can thus be an important constraint on the activity of its ectotherm consumers.

Key words: activity; ants; arthropods; biogeography; latitudinal gradient; metabolism; net primary productivity (NPP); temperature.

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INTRODUCTION

Community properties such as abundance and diversity vary from place to place, and considerable effort has been made to understand this geography (e.g., Rosenzweig 1995). One such community property, thus far poorly explored, is consumer activity, defined here as the rate that individuals move through their environment. Activity is measured using a variety of methods (including pitfall traps, baits, and camera traps; Southwood 1978, O'Connell et al. 2010, Gibb et al. 2017). Understanding the constraints on consumer activity should help us better understand variation in the rates that predators find their prey, herbivores find their host plants, scavengers find detritus, and mutualists find each other. Here, we introduce a simple model of consumer activity and test it with a recent geographic dataset (Roslin et al. 2017).

Imagine a pitfall trap that tallies all the individuals of a beetle population that fall into the trap over 24 h (i.e., individuals/time). Doubling beetle velocity (m/h), *ceteris paribus*, should roughly double beetle activity measured by the trap. An ectotherm's velocity, in turn, is constrained by temperature, with that constraint relaxing in an accelerating fashion as temperature rises, before reaching a threshold (Bennett 1990, Hurlbert et al. 2008, Kaspari et al. 2016). How this temperature–velocity relationship scales up to activity in communities is less explored. Global change models typically assume organisms start activity above a thermal minimum and cease activity above a thermal maximum (Buckley and Kingsolver 2012) although it should increase or even accelerate with temperature (as it does, for example, with frog vocalizations; Gerhardt 1978, Gunderson and Leal 2015). Indeed, activity of an ant community at baits showed the predicted acceleration with environmental temperature at daily and seasonal time scales (Prather et al. 2018). We predicted a similar relationship between ectotherm activity—summed over days—and ecosystem temperature. We know of no such geographical analysis of temperature as a key constraint of activity at geographical extents.

Likewise, doubling the abundance (individuals/ha) of the beetle population, *ceteris paribus,* should also roughly double the number of individuals that fall into a trap in a given amount of time. Species–energy theory (Wright 1983) assumes that that net primary productivity (NPP, g Carbon·m^{-2}·yr^{-1}) sets an upper limit to the number of individuals an environment can support. This was the case in one geographical study of 49 ant communities from deserts to rainforests (Kaspari et al. 2000) where NPP accounted for ca. half the geographic variation in colony abundance.

Despite its importance in driving population interactions and ecosystem services, standardized geographic datasets on consumer activity are rare. Recently, an experiment distributed across ecosystems from tundra to rainforest placed model clay caterpillars in vegetation, returning days later to record which had been discovered (i.e., chewed on) by different groups of consumers (Roslin et al. 2017). They noted that the strongest trend was among arthropods, notably ants, whose activity greatly increased toward the tropics. Here, like Prather et al. (2018), we harness the explanatory power of continuous variation in NPP and the maximum summer monthly temperature (when most of the studies were conducted) to test the hypothesis that NPP and temperature co-constrain the geography of activity, and in doing so, provides a possible mechanism for their latitudinal gradient in activity.

Methods

The above model predicts how geographic patterns in consumer activity can be constrained by NPP and by environmental temperature. We discuss the source of each in turn.

Consumer activity

In 2013 and 2014, a geographically distributed experiment was organized by a variety of laboratories working across 31 sites spanning forests, tundra/shrublands, and wetlands, and on every continent but Antarctica (summarized here from details in Roslin et al. 2017). These sites were chosen to experience minimal anthropogenic disturbance (e.g., national parks and other protected reserves). The experiment placed model caterpillars made of clay in local vegetation to quantify the rate they were discovered by consumers. Those trials outside the aseasonal tropics were run in the warm summer months (but did not simultaneously record temperature). At each site, in each of five 3 × 4 m plots, 20 clay caterpillars were set out on local vegetation. The duration of the experiment varied but was typically 96 h, allowing investigators to estimate a final rate of caterpillar discovery per day—our measure of activity. Marks in the clay were attributed to a variety of agents (e.g., lizards, mammals, gastropods, and birds, Low et al. 2014), but we focus here on one large consumer class, the arthropods, which the authors noted were mainly ants.

We calculated two measures of activity (both in units of caterpillars discovered per day): the mean across five sample plots for the site (which assumes temperature and NPP are main drivers of activity) and the maximum rate recorded for the five plots (the focus of this study, assuming NPP and temperature are constraints on activity).

Geographic data on NPP and temperature

We used the latitude/longitude data for each site (provided at four significant digits in decimal degrees) to extract both the NPP and the mean temperature across the 12 months. We used the Application for Extracting and Exploring Analysis Ready Samples (https://lpdaacsvc.cr.usgs.gov/appeears/) to extract the MODIS TERRA and AQUA NPP (MOD17A3H and MYD17A3H, https://doi.org/10.5067/modis/mod17a3h.006) and land surface temperature data (MOD11A2 and MYD11A2, https://doi.org/10.5067/modis/mod11a2.006) from collection 6, at 500 m and 1000 m spatial resolution, respectively. The NPP product is an annual product, while the land surface temperature product is delivered every 8 d, with 46 observations per year.

Table 1. General linear models (type III sum of squares) testing the prediction that the mean and maximum activity of arthropods across 31 sites, from tundra to rainforest, increases with net primary productivity (NPP) and maximum monthly temperature in a manner that leaves no further variation accounted for by latitude.

Source	df	SS	F	Pr > F	Parameter	Est.	SE	t	Pr > t
Max activity									
Temperature	1	0.005	1.35	0.255	Intercept	−0.066	0.091	−0.73	0.474
NPP	1	0.026	6.83	0.015	Temperature	0.003	0.003	1.16	0.255
|Latitude|	1	0.001	0.26	0.613	NPP	0.103	0.039	2.61	0.015
Error	27	0.103			Latitude	0.000	0.001	0.51	0.613
Mean activity									
Temperature	1	0.002	0.83	0.3711	Intercept	−0.011	0.074	−0.15	0.883
NPP	1	0.006	2.47	0.1275	Temperature	0.002	0.002	0.91	0.371
Latitude	1	0.000	0.04	0.8478	NPP	0.050	0.032	1.57	0.128
Error	27	0.068			Latitude	0.000	0.001	−0.19	0.848

We used the average of the TERRA and AQUA MODIS estimates for a site's NPP (annual g $C{\cdot}m^{-2}{\cdot}yr^{-1}$). In three arctic sites where no MODIS NPP data were available (at 68–75° N latitude in Finland, Alaska, United States, and Greenland), we substituted the lowest value for NPP in an arctic dataset (160 $gC{\cdot}m^{-2}{\cdot}yr^{-1}$, 61 N latitude, Yukon, Canada).

The experiments were run in summer months in the temperate sites, when temperatures were at their highest. We thus used each site's maximum of its 12 mean monthly temperatures (typically July) as representative of the air temperature most likely experienced by the ectotherms over the four days that the experiments typically ran. These values ranged fivefold, from 4.6° to 29°C, and were highly correlated with mean monthly temperature (r = 0.94).

Analysis

We used a general linear model (GLM, SAS 2009) to evaluate the hypothesis that the mean and maximum activity of arthropods across 31 sites, both normally distributed (Kolmogorov-Smirnov D = 0.1, P > 0.15), from tundra to rainforest, increases with NPP and maximum monthly temperature in a manner that leaves no further variation accounted for by latitude.

Results

Across the 31 sites, maximum monthly temperature varied fivefold (4.6–29.5°C). Net primary productivity varied 19-fold (from 85 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ to 1617 $gC{\cdot}m^{-2}{\cdot}yr^{-1}$). Mean arthropod activity varied from 0 to 0.23 caterpillars discovered per day; maximum arthropod activity varied from 0 to 0.30 caterpillars discovered per day.

Maximum activity increased linearly with NPP but not temperature (GLM P = 0.015 vs. P = 0.26, Table 1, Fig. 1) in a way that left no variation accounted for by latitude (P = 0.64). Mean activity showed a similar pattern, but the contribution of NPP did not reach significance at P < 0.05 (Table 1).

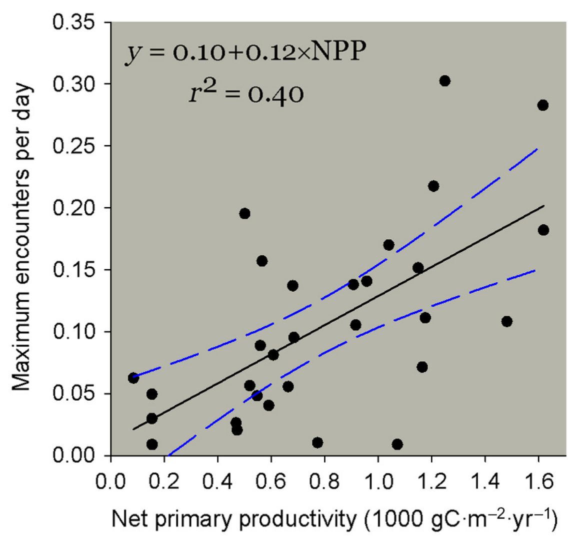

Fig. 1. A measure of arthropod activity—the discovery rate of clay caterpillars in the field—increases linearly (±95% CI) with net primary productivity estimated by MODIS satellites. Inset equation is from OLS regression. Sites represent ecosystems from tundra to rainforest and from −30 to 74 latitude.

Discussion

The collective activity of organisms in an ecosystem—driven by the number of organisms and their per-capita metabolism—is a fundamental but relatively unexplored variable for geographical ecologists. We find that in a collection of sites ranging from tundra to rainforests, NPP—a measure of energy available to consumers and a constraint on abundance (Kaspari et al. 2000, Meehan et al. 2004)—can account for up to 40% of the observed variation in the rate that arthropods encounter a clay model embedded in vegetation. By doing so, we provide a potential biological mechanism for the geographic pattern documented by Roslin et al. (2017). Temperature, which along with precipitation can co-constrain NPP, failed to account for further variation. As discovery rates increased linearly with NPP, our results suggest that consumer activity (a significant driver of ecosystem services and population interactions) can have a relatively simple relationship to the rate that energy enters the ecosystem.

The role of geographic drivers such as temperature is well established as constraints to species ranges (Root 1988, Mainali et al. 2015). Our failure to find a clear temperature effect on activity may reflect the many ways this could come about. Temperature may regulate abundance by co-constraining NPP (Rosenzweig 1968), by constraining the productivity of ectotherms (Kaspari et al. 2000) as well as constraining velocity—the focus of our model. These multiple actions of temperature—acting at multiple spatial and temporal scales (Angilletta 2009, Kaspari et al. 2015) —must be further considered and quantified in future such experiments.

Similarly, we note that NPP is best viewed from these data as a constraint to ectotherm activity, since the mean activity across the five plots per site was not as well predicted by NPP. Other contingencies that lower activity below the maximum—like local weather during these short-term experiments—are not captured by our dataset (i.e., NPP is less likely to vary daily than maximum daily temperature). In the same vein, highlighting the role of NPP may also help reveal other factors shaping consumer activity, like geographic variation in predators that suppress activity in their consumer prey (Lima and Dill 1990). Understanding how drivers at different spatial grains, and different time scales, combine to generate activity is an obvious and fruitful next step.

Two distributed experiments (Jeanne 1979, Roslin et al. 2017) found greater bait discovery toward the tropics; both interpreted their results as evidence for latitudinal gradients in ant predation. However, ants are ubiquitous scavengers that explore their environment looking for potentially edible detritus (Del Toro et al. 2012, Griffiths et al. 2018). We thus suggest that it is more parsimonious to register an ant's mandible marks (and, in the case of Jeanne 1979, the disappearance of dead wasp larvae) as an encounter, not a killing. In this light, both studies would then address a different, but still fundamental, question: What is the geography of ectotherm activity? Fortunately, we are in an increasingly good place to answer that question as datasets on consumer activity accumulate from pitfall traps, baits, and camera traps (Southwood 1978, O'Connell et al. 2010, Gibb et al. 2017). By focusing on geographic drivers of abundance and velocity, we hope to clarify an important bioclimatic constraint for those exploring the more complex question of geographical gradients in population interactions (Schemske et al. 2009, Johnson and Rasmann 2011, Moles et al. 2011). Future work linking activity to bioclimatic variables, and ultimately measuring the geography of abundance and velocity, will help get at this important question.

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