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Determinants of intra-annual population dynamics in a tropical soil arthropod

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Abstract

Studies on inter-annual dynamics of populations from temperate regions have shown that density dependence and climate effects are relatively common, albeit weak. Yet, for short-lived organisms, intra-annual variation may be at least as important. Furthermore, tropical species commonly experience temperatures close to their upper thermal limit and thus may be more likely to experience heat stress. Here, we used the soil mite *Rostrozetes ovulum* to investigate the drivers of intra-annual population dynamics in an Amazonian rain forest. We sampled 3,600 soil cores from 20 transects during 13 months, obtaining 180 mite counts. Next, we built a dynamic N-mixture model accounting for different detection probabilities between soil types. In a Bayesian framework, we used this model to estimate (a) the strength of density dependence and (b) per capita growth rates, which were then tested against environmental variables. We found that the intra-annual population dynamics of *R. ovulum* were weakly density dependent. Further, per capita growth rates increased with resource supply (litterfall) and decreased with maximum temperature over much of the observed thermal range, although these effects explained relatively little variance. Yet, the seasonal correlation between these factors created a trade-off, so that realized population growth was highest when neither resource supply nor thermal suitability was optimal. Overall, our results suggest that the mechanisms shaping soil animal population dynamics may be surprisingly similar across latitudes. Our model offers a starting point for analyses of soil animal counts when extraction from soil samples is imperfect.

KEYWORDS
ecological niche, fitness, Gompertz model, population regulation, soil invertebrate, state-space model

1 | INTRODUCTION

In the last decade, the increasing availability of density time series and improved analytical methods have fostered large meta-analyses of the factors driving population dynamics in the field. Accordingly, some patterns have emerged. For instance, per capita growth rate often decreases as population density increases, but this effect is typically weak (Knape & de Valpine, 2012; Ziebarth, Abbott, & Ives, 2010) and decreases from fast to slow life histories (Herrando-Pèrez, Delean, Brook, & Bradshaw, 2012). Density dependent population growth suggests that intrinsic processes such as intraspecific competition regulate populations to some degree, although other processes (e.g., predation, parasitism) could have the same effect (Sibly & Hone, 2002). Further, population dynamics are commonly but weakly affected by climate (García-Carreras & Reuman, 2011; Herrando-Pérez, Delean, Brook, Cassey, & Bradshaw, 2014; Knape & De Valpine, 2011). Climate can affect population growth either directly through abiotic conditions (e.g., temperature and rainfall), or indirectly by controlling food supply

(White, 2008). However, these conclusions are largely based on yearly time series of populations from Europe and North America. Therefore, the extent to which they apply to finer temporal scales and low-latitude populations is unclear.

Consideration of finer temporal scales is important because most species are relatively short-lived and have multiple generations per year (e.g., arthropods), suggesting greater dependence on environmental seasonality (Betini, Griswold, & Norris, 2013). Indeed, the predictability of yearly density time series tends to decrease from longer- to shorter-lived organisms (Knape & De Valpine, 2011). Yet, even in longer-lived species, intra-annual variation may have significant impacts on between-year population dynamics (Marra, Cohen, Scott, Rutter, & Christopher, 2015), and the processes shaping inter- and intra-annual dynamics can differ (Karels & Boonstra, 2000).

The bias of population data toward mid- to higher latitudes complicates global inferences about both density dependence and climate effects (Cohen, Lajeunesse, & Rohr, 2018; Herrando-Pérez et al., 2014). For instance, if density dependence is generally driven by intraspecific competition, then its strength may be weaker in the tropics due to higher productivity and, thus, higher resource supply to consumers (Gillman et al., 2015). However, tropical ecosystems experience significant seasonality in productivity due to seasonal rainfall and insolation patterns (Caldararu, Palmer, & Purves, 2012; Wagner et al., 2017), and abiotic seasonality itself can affect population dynamics, for example, by limiting reproduction to periods of optimal moisture (Brown & Shine, 2006). Moreover, although thermal seasonality is modest in the tropics, tropical species often have narrow thermal tolerances and experience naturally higher temperatures, increasing the likelihood of heat stress (Deutsch et al., 2008; Kingsolver, Diamond, & Buckley, 2013). Altogether, the links between abiotic conditions and productivity may impose a trade-off on population growth. For instance, productivity peaks during hotter months over vast areas of tropical forest (Wagner et al., 2017), suggesting that higher resource supply may be offset by heat stress.

Much of animal abundance occurs in the litter–soil interface, where densities of arthropods such as mites and springtails can easily reach tenths to hundreds of thousands of individuals per square meter (Takeda & Abe, 2001). Studies from temperate regions have suggested important roles for density dependence and temperature in shaping soil animal population dynamics (Choi, Moorhead, Neher, & Ryoo, 2006; Ferguson & Joly, 2002; Kuznetsova, 2007; Pfingstl, 2013; Stamou & Sgardelis, 1989; Stamou, Stamou, Papatheodorou, Argyropoulou, & Tzafestas, 2004), whereas studies from tropical regions have suggested a major role for hydrology, for example, rainfall and floods (Burgess, Ponder, & Goddard, 1999; Frith & Frith, 1990; Levings & Windsor, 1984; Pequeno & Franklin, 2014; Pequeno, Franklin, Norton, de Morais, & Guilherme, 2017; Wiwatwitaya & Takeda, 2005). However, in many cases, the potential for confounding effects arising from natural correlations among environmental variables has not been accounted for. Moreover, extraction of soil fauna from soil samples typically underestimates true densities (Andre, Ducarme, & Lebrun, 2002), which can strongly bias estimates of

strength of density dependence (Dennis, Ponciano, Lele, Taper, & Staples, 2006; Knape & de Valpine, 2012; Lebreton & Gimenez, 2013). Addressing these issues should improve our understanding of soil animal population dynamics.

To answer these questions, we used the parthenogenetic soil mite, *Rostrozetes ovulum* (Berlese, 1908) (Oribatida: Haplozetidae). This cosmopolitan arthropod feeds on leaf litter (i.e., primary decomposer) (Illig, Langel, Norton, Scheu, & Maraun, 2005) and is especially abundant in tropical forests, where it often dominates local oribatid mite assemblages (Moraes, Franklin, Morais, & Souza, 2011). In central Amazonia, *R. ovulum* takes around six weeks to develop from egg to adult, producing clonal offspring during the next three months (Beck 1969). In the same region, adults peak in abundance for two to three months (Pequeno et al., 2017), suggesting an average adult life span of similar duration in the field and, thus, an average life cycle of four to five months.

We performed spatially replicated sampling of *R. ovulum* over one year across a central Amazonian rain forest landscape. Observed counts were then used to address three complementary questions. First, are *R. ovulum's* intra-annual population dynamics density dependent? Using a Bayesian framework, we built and fit a state-space model of density dependent population growth. Our model allowed simultaneous estimation of the strength of density dependence and of the true densities associated with observed counts, while accounting for imperfect detection. We hypothesized that *R. ovulum* should experience relatively strong density dependence, as suggested by its short life cycle (Herrando-Pèrez et al., 2012) and by the generally lower density of soil microarthropods in the tropics relative to temperate regions (Takeda & Abe, 2001). Second, what are the relative contributions of resources and abiotic conditions to intra-annual variation in *R. ovulum's* population growth rate? We used the estimates of true density to calculate per capita growth rates over space and time, and then assessed the extent to which they could be explained by resource supply (litterfall), rainfall, and temperature. We hypothesized that population growth should increase with litterfall, but generally decrease with temperature, assuming that tropical species operate near their upper critical thermal limit (Deutsch et al., 2008; Kingsolver et al., 2013). Likewise, we expected population growth to decrease with rainfall due to impaired survival and/or reproduction by prolonged waterlogging and hypoxia (Pequeno et al., 2017). Lastly, is *R. ovulum* population growth subject a trade-off between food supply and thermal suitability? We expected litterfall to be highest during hotter months (Wagner et al., 2017), so that population growth would be highest when neither food supply nor temperature were optimal.

2 | METHODS

2.1 | Study site

We sampled *R. ovulum* in a 800-ha forest remnant in Manaus, northern Brazil (03°04′34″S, 59°57′30″W), most of which belongs to the Federal University of Amazonas. Mean monthly air temperature

varies from 24 to 30°C, and annual rainfall is around 2,200 mm, with a drier season (monthly rainfall below 100 mm) from July to October. Local relief features a dense drainage system where altitude varies from *ca.* 40 to 80 m a. s. l. This creates an alternation between plateaus and valleys with contrasting environmental conditions. In plateaus, soils are clayish and the water table is many meters below ground level, whereas in valleys soils are sandy and the water table is shallow, thus causing waterlogging and short-term floods during heavy rains (Hodnett, Vendrame, Filho, Oyama, & Tomasella, 1997). Plateaus also tend to have higher plant biomass (Castilho et al., 2006) and to produce and accumulate more litter than valleys (Luizão et al., 2004).

2.2 | Data collection and assembly

We sampled 20 transects, each 20-m long, distributed over the forest landscape from June 2014 to June 2015. Ten transects were in valleys, while the remaining transects were located on plateaus, at least 150 m away from any drainage catchment. At each transect, one soil sample was taken each meter using an aluminum soil corer (3.5 × 3.5 × 5 cm), covering a total of 245 cm^2. This material was taken to the laboratory, where the soil fauna was extracted using a Berlese–Tullgren apparatus (Franklin & Morais, 2006). Each soil core was put in a sieve with mesh size 1.5 mm, which was placed in a plastic funnel. Then, the funnel was put into a wooden box, where it was fitted through a perforated polystyrene board, with a glass vial filled with 95 percent alcohol below it. Next, the box was gradually heated from ambient temperature (ca. 27°C) to 35–40°C using light bulbs (25 W). Vials were checked daily for fallen animals. Heating lasted until the core was completely dry and animals stopped falling into the vial (7 to 10 days). The collected material was surveyed under a stereomicroscope for *R. ovulum*. Adult individuals were identified with the aid of a key for Neotropical oribatid mites (Balogh & Balogh, 1990), counted and preserved in 95 percent alcohol. Transects were sampled on nine months (June to September and November 2014; and January, March, April, and June 2015). Therefore, the spatiotemporal coverage of our study was 20 transects × 13 months = 240 spatiotemporal units, of which 20 transects × 9 surveys = 180 counts were recorded from a total of 3,600 soil cores.

Environmental seasonality data were obtained from research sites nearby the study area or estimated from such sites. Temperature and rainfall data were gathered online from the nearest station of the Brazilian Institute for Meteorology (INMET), which is 1 km from the study area. We extracted daily readings to compute cumulative rainfall (mm) and maximum daily air temperature (°C) for each transect and month covered by our sampling. In central Amazonia, monthly means of air and soil temperatures are well correlated ($r = 0.82$, $n = 18$) (Martius et al., 2004), and spatial variation in soil temperature within closed-canopy forests is negligible, with no difference between plateaus and valleys (Zanchi et al., 2014). Thus, air temperature is

a reasonably proxy for soil temperature. We used the maximum rather than the mean because it is more variable and more likely to impact the mite's physiology (Pequeno, Franklin, Norton, & De Morais, 2018).

Litterfall was estimated using time series of monthly litter production per habitat (plateau and valley) from the Cuieiras Biological Reserve (22,735-ha), 60 km from the study area (Conceição, 2017). Litterfall was sampled with 30 PVC collectors (50 × 50 cm) randomly placed 50 cm above ground in each habitat, between May 2004 and December 2005, January 2009 and December 2010, and November 2014 and August 2015. In Amazonia, litterfall peaks in the drier season and has been successfully modeled as an interaction between light and water availability (Caldararu et al., 2012; Wagner et al., 2017). There is also evidence that litterfall tends to be higher in plateaus than in valleys (Luizão et al., 2004). Thus, we obtained meteorological data from the INMET station corresponding to the litterfall measurements provided by Conceição (2017) to model the latter as a function of (a) monthly sunlight hours, monthly cumulative rainfall and their interaction, (b) habitat (dummy variable: valley = 0, plateau = 1), and (c) time (months, coded as integers spanning the temporal coverage of the data) in order to account for any long-term trend. Using a generalized linear model with gamma-distributed errors and log link (a standard choice for strictly positive, continuous variables; Zuur, Ieno, Walker, Saveliev, & Smith, 2009), we found support for the sunlight × rainfall interaction ($p = .012$), as well as for the independent effects of habitat ($p = .041$) and time (0.00015). The resulting model (log *litter* = 5.82 + 0.0053 × *light* +0.00098 × *rain* +0.11 × *habitat* – 0.0025 × *time* – 0.000014 × *light*×rain, $n = 108$) had a correlation between observed and predicted values of $r = 0.79$, and was used to predict the expected litterfall (g/m^2) for each of our spatiotemporal units, given the corresponding environmental conditions. The relationship between litterfall and climate factors is consistent over central Amazonia (Caldararu et al., 2012; Wagner et al., 2017), and so it is reasonable to assume that such predictions are informative regarding seasonal and between-habitat variation of litterfall in our study site.

2.3 | Population modeling

All analyses were performed in R 3.4.4 (R Core Team, 2018) and JAGS (Plummer, 2003). To describe the main features of *R. ovulum's* population dynamics while accounting for imperfect detection, we employed state-space modeling (Dennis et al., 2006; Lebreton & Gimenez, 2013). Population state-space models describe observed counts as realizations of an (imperfect) observation process, which is itself a function of a latent population dynamic process. They allow simultaneous estimation of detection error, population dynamic parameters, and true population densities from one or multiple count time series.

Here, we elaborated on a recent class of such models known as dynamic N-mixture models (Bellier, Kéry, & Schaub, 2016; Dail & Madsen, 2011; Hostetler & Chandler, 2015). Such models have three main components: (a) The observed count at site *i* and time *t*

($y_{i,t}$) is modeled as a realization of a binomial distribution with detection probability p and number of trials equal to the true density, $N_{i,t}$ (i.e., the "N-mixture"). This captures the detection process of soil fauna, as only a fraction of the individuals in soil cores is actually extracted (Andre et al., 2002); (b) $N_{i,t}$ is modeled as a realization from a Poisson distribution with a given mean, which can be conditional on any function of interest, for example, classic population dynamic equations (Hostetler & Chandler, 2015). We used the linearized, discrete-time Gompertz equation, a standard model of density dependent population dynamics: $\log N_{i,t} = a + c \log N_{i,t-1}$ (Dennis et al., 2006; Knape & de Valpine, 2012; Lebreton & Gimenez, 2013). Here, a is the intrinsic rate of increase (in log scale), and c is the strength of density dependence. When $c = 1$, dynamics are density independent; the lower the value of c, the stronger the density dependence; (c) the initial, unobserved density $N_{i,1}$ is modeled as a realization from a Poisson distribution with a mean λ across sites.

We considered two possible extensions of this model. First, in upland central Amazonian forest, soil invertebrates reproduce and grow more or less continuously over the year (Adis & Junk, 2002). If population change occurs mainly at a temporal scale finer than that of our observations, then $N_{i,t}$ will be overdispersed relative to the expectation from a Poisson distribution (Hostetler & Chandler, 2015). To capture this effect, we introduced a "hidden" time step in the model: Each observed count $y_{i,t}$ was a function of $N_{i,t}$, the latter being a function of another unobserved density within the same month, $N'_{i,t}$. Second, extraction of oribatid mites with Berlese–Tullgren funnels has an absolute efficiency of 70%–100% where measured, but this can be considerably lower in soils poor in organic matter, such as sandy soils (Andre et al., 2002). Because plateaus in central Amazonia have clayish soils and valleys have sandy soils, we also modeled distinct detection probabilities for each habitat. Therefore, our full model was as follows (Supporting Information):

$$N_{i,1} \sim \text{Poisson}\left(\lambda\right) \tag{1}$$

$$N'_{i,t} \sim \text{Poisson}\left(\exp\left(a + c \log N_{i,t-1}\right)\right) \tag{2}$$

$$N_{i,t} \sim \text{Poisson}\left(\exp\left(a + c \log N'_{i,t}\right)\right) \tag{3}$$

$$y_{i,t} \sim \begin{cases} \text{Binomial}\left(p_{\text{plateau}}, N_{i,t}\right) \\ Binomial\left(p_{\text{valley}}, N_{i,t}\right) \end{cases} \tag{4}$$

We also evaluated three simplifications of this model: (a) the model excluding the hidden time step (Equation 2); (b) the model excluding variation in detection probability (Equation 4); and (c) the basic model, excluding both the hidden time step and variation in detection probability. Each model was fit using Bayesian inference in JAGS, called from R with package "R2jags" (Yu-Sung & Yajima, 2015). We assumed vague priors for all parameters: $\lambda \sim$ Gamma

(0.005, 005); $a \sim$ Gamma(0.5, 0.5); $c \sim$ Normal(1, 0.1); $p \sim$ Beta(1, 1). We ran two Markov chains for 475,000 iterations each, using a thinning rate of 400 and discarding the first 75,000 iterations as burn-in. Months without surveys had counts coded as "NA"; their unobserved densities were automatically estimated by JAGS along those of surveyed months. Convergence was evaluated by checking trace plots and whether the Brooks–Gelman–Rubin statistic was < 1.1 for all parameters. The model with lowest deviance information criterion (DIC) was judged the most supported one, and we used this model to estimate the strength of density dependence (c) and to obtain estimates of true densities ($N_{i,t}$). As a measure of goodness-of-fit, we calculated the squared correlation between observed counts and their predictions according to the deterministic components of the model (i.e., mean initial density for the first time step and densities predicted for further time steps, multiplied by detection probability). We used the 95% credible interval (95%CI) of c to test for density dependence (i.e., whether it excluded 1) and for different detection probabilities between habitats (i.e., whether they did not overlap). Also, we assessed bias and coverage under the best model with simulations (Figure S1).

In principle, we could add environmental covariates directly to these models. However, adding further parameters caused Markov chains to fail to converge over several hundreds of thousands of iterations. Indeed, parameter estimability of state-space models decreases rapidly with model complexity, especially with relatively short time series (Auger-Méthé et al., 2016; Lebreton & Gimenez, 2013). Nonetheless, density estimates from dynamic N-mixture models appear to be relatively robust to model misspecification (Bellier et al., 2016; Dunham & Grand, 2016). Thus, we used estimates of population density from the best model to calculate per capita growth rates (pgr):

$$pgr = \log \frac{N_{i,t}}{N_{i,t-1}} \tag{5}$$

Then, we tested for environmental effects on pgr with standard frequentist methods. We used a linear model with normal errors accounting for temporal autocorrelation, fit with function gls() from the "nlme" package in R. Autocorrelation was modeled as a first-order autoregressive structure within transects, using function corAR1(). The response variable was pgr, and predictors were maximum temperature, cumulative rainfall, and cumulative litterfall. Litterfall was log-transformed to account for nonlinear, monotonic relationships, and temperature included a quadratic term to account for unimodal relationships. We also included habitat (plateau or valley) as a fourth predictor, to control for its possible effect. For each predictor, we used the R package "visreg" to create conditional plots showing variation in pgr in relation to each predictor while holding remaining predictors constant, as well as a contour plot to visualize the joint response of pgr to the main predictors (Breheny & Burchett, 2017). Lastly, we assessed the proportion of variance explained independently by each predictor using hierarchical partitioning (MacNally, 2000), implemented by function hier.part() from the R package "hier.part."

TABLE 1 Summary statistics of posterior distributions inferred for the parameters of the dynamic N-mixture model

Parameter	Posterior mean	95% credible interval
λ	2.906	1.633 to 4.806
a	0.248	0.087 to 0.398
c	0.874	0.798 to 0.947
$p_{plateau}$	0.448	0.345 to 0.563
P_{valley}	0.174	0.109 to 0.264

Note: λ: mean initial density; a: intrinsic rate of increase (in log scale); c: strength of density dependence; $p_{plateau}$: detection probability in plateau soil cores; p_{valley}: detection probability in valley soil cores

3 | RESULTS

The full model (DIC = 634.4) was favoured over the basic model (DIC = 847.5) and those including only the hidden time step (DIC = 644.7) or habitat-specific detection probabilities (DIC = 914.3). Further, the deterministic component of the full model predicted observed counts of *R. ovulum* relatively well (r^2 = .69). This model revealed that there was detectable density dependence in *R. ovulum's* intra-annual population dynamics (i.e., c < 1), but the strength of density dependence was relatively weak, with c only slightly smaller than one (Table 1; Figure 1). Detection probabilities were moderate to low and differed between habitats: Extraction from plateau soil cores was over twice more effective than extraction from valley soil cores (Table 1). Estimated densities averaged 3.94 ± 5.48 (mean ± *SD*) individuals over all transects and months, ranging between 0 and 56.68 individuals (Figure 1). This is equivalent to 160.89 ± 223.72 individuals per square meter and month, on average, ranging between 0 and 2,313.63 individuals. Simulations showed that bias was minimal, and coverage was reasonable for most parameters, whereas detection probability in valleys was overestimated (Figure S1).

Estimated per capita growth rate was significantly related to different environmental variables (Table 2). Specifically, *R. ovulum's pgr* increased with litterfall and rainfall (Figure 2a,c). In parallel, *pgr* was a quadratic function of maximum temperature, changing little between 34 and 35 °C and declining above the latter (Figure 2b). By contrasts, there was no difference in *pgr* between plateaus and valleys, on average (Figure 2d).

Hierarchical partitioning indicated that environmental variables explained 25% of the variance in *R. ovulum's pgr*. The predictors with highest explanatory power were maximum temperature, independently accounting for 15% of the variance, and litterfall, which explained another 6%; rainfall and habitat had negligible explanatory power (<1%) (Table 2). The remaining variance could not be attributed to any particular predictor, reflecting correlations among them. Further, optimal conditions for population growth under the joint effects of maximum temperature and litterfall did not occur throughout the study: When litterfall was optimal, maximum temperature was too high, whereas when the latter was optimal, the former was too low (Figure 3).

4 | DISCUSSION

Our modeling of the intra-annual population dynamics of the soil mite *Rostrozetes ovulum* in a tropical rain forest produced three main findings. First, dynamics were density dependent (i.e., c < 1), albeit to a low degree (c = 0.87). Second, the mite's per capita growth rate was affected by environmental factors, but these explained relatively little variance. Third, realized growth rate was highest when neither litterfall nor maximum temperature were optimal due to natural correlations between them. These conclusions are strengthened by our spatial replication of time series and explicit consideration of imperfect detection. Detection probability was lower in sandy valleys than in clayish plateaus, consistent with the expected difference in extraction efficiency
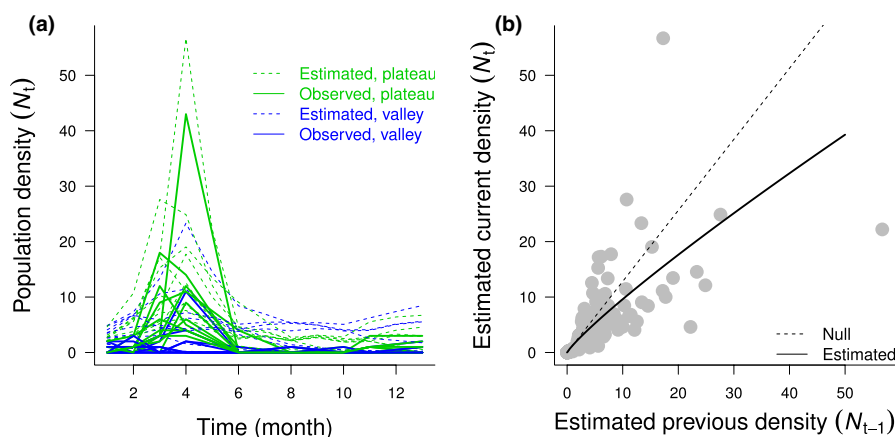

FIGURE 1 Intra-annual population dynamics of the soil mite *Rostrozetes ovulum* in a tropical rain forest landscape in central Amazonia, according to the fitted dynamic N-mixture model. (a) Observed and estimated population density over the study period. Each solid line represents one transect over months (20 transects × 9 surveyed months = 180 observed counts). (b) Relationship between current and previous estimated density. The dashed line represents the null hypothesis of no density dependence (i.e., slope of 1); each point represents an estimate for a given transect in a given month (n = 240)

TABLE 2 Linear model relating per capita growth rate of the soil mite *Rostrozetes ovulum* to environmental variables ($n = 240$)

Parameter	Estimate	t	p	Variance share (%)
Intercept	−97.703	–	–	–
Temperature	5.412	4.070	**<.001**	7.5
Temperature^2	−0.078	−4.164	**<.001**	7.4
log Litterfall	1.059	8.625	**<.001**	6.0
Rainfall	0.001	2.772	**.006**	0.9
Habitat	−0.109	−0.884	.377	0.000

Note: A first-order autoregressive correlation structure was imposed on residuals within transects to account for temporal autocorrelation; the autocorrelation coefficient ρ was estimated as 0.63. Habitat was coded as a dummy variable (0: plateau; 1: valley). Independent variance shares were determined with hierarchical partitioning. The model explained 25% of the variance in *pgr*, of which 3% was not attributed to any particular predictor, reflecting correlations among them
Bold values indicate statistically significant values ($P < 0.05$.)

between these soil types (Andre et al., 2002). Indeed, simulations of model performance suggested that detection probability in valleys was even lower than our estimate (Figure S1). Overall, our results suggest that both density dependent and independent mechanisms contributed to the seasonal population dynamics of the mite.

Density dependence could be due to any factor that decreases survival and/or fecundity at higher densities, for example, intraspecific competition, predation, or parasitism (Sibly & Hone, 2002). The increase in *R. ovulum's pgr* with litterfall suggests that at least part of the observed density feedback reflects competition

for food. Indeed, the slightly saturating response of *pgr* to litterfall (Figure 2a) is consistent with litter manipulation experiments in forests: Litter removal often reduces soil fauna density, whereas litter addition has little or no effect (Ashford et al., 2013; Sayer, 2006). By contrast, oribatid mites are often assumed to live in "enemy-free space," given their hardened cuticles and production of repellent chemicals (Peschel, Norton, Scheu, & Maraun, 2006). Yet, in tropical forests, ants may regularly prey upon at least some oribatid species (Wilson, 2005). The role of parasitism is unclear; oribatid mites are hosts of many parasites, but whether they cause density dependent mortality is unknown (Van Der Geest, Elliot, Breeuwer, & Beerling, 2000).

Per capita growth rate was a unimodal function of maximum temperature, but mainly declined along the observed thermal range. Interestingly, maximum temperature had the highest explanatory power among the analyzed environmental variables, even though the observed thermal range was relatively narrow (Figure 2b). This is consistent with tropical species having narrow thermal tolerances and operating near their upper thermal limit (Deutsch et al., 2008; Kingsolver et al., 2013). In contrast, rainfall and habitat had negligible effects, refuting our hypothesis that waterlogging could drive population decline. The lack of relationship between population growth and these variables may result from *R. ovulum's* relatively high submersion tolerance (Pequeno & Franklin, 2014).

Together, these results suggest a mechanistic interpretation for the main patterns observed in *R. ovulum* counts. The highest counts occurred in plateaus during drier, hotter months, whereas both habitats converged toward low counts during wetter, cooler
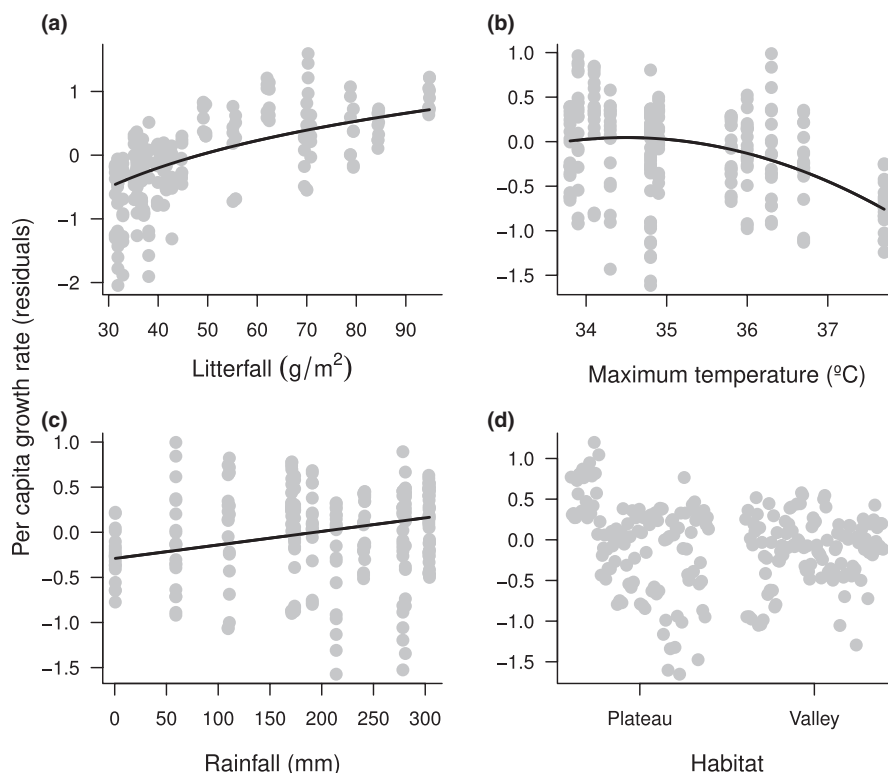

FIGURE 2 Environmental effects on the population growth of the soil mite *Rostrozetes ovulum* in central Amazonia. Conditional plots show the effect of each predictor on the partial residuals of per capita growth rate, controlling for the effects of remaining predictors. Each point represents a given transect in a given month ($n = 240$). Solid lines indicate model fits
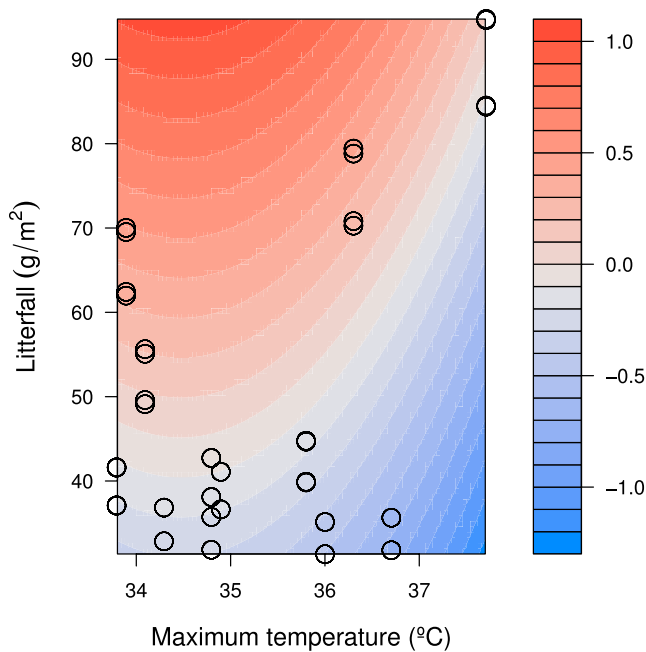
FIGURE 3 Response of the soil mite *Rostrozetes ovulum* to resource supply (litterfall) and maximum temperature in central Amazonia. Colors indicate the expected per capita growth rate for each combination of predictors; the reddish area represents environmental combinations where growth is positive and, therefore, comprises *R. ovulum's* niche regarding these variables. Circles indicate combinations of predictor values observed during the study

months (Figure 1a; Pequeno et al., 2017). The difference between habitats reflects partly the higher extraction efficiency in clayish plateaus, and partly the higher litterfall in that habitat. In parallel, increasing litterfall and rising temperatures shape a seasonal density peak: Population growth is simultaneously fostered by litterfall and constrained by maximum temperature. Eventually, increasing densities strengthen intraspecific competition, which further limits population growth, causing densities to fall back to levels similar those before the peak (Figure 1a). Because litterfall tends to be highest during hotter months, *R. ovulum* experiences a trade-off between resource supply and thermal suitability: The predicted optimal conditions for growth never occur, and actual population growth is highest when neither litterfall nor maximum temperature is optimal (Figure 3).

Previous studies have suggested that, in temperate regions, soil microarthropod population dynamics are mainly shaped by density dependence and temperature (Choi et al., 2006; Ferguson & Joly, 2002; Pfingstl, 2013; Stamou & Sgardelis, 1989; Stamou et al., 2004). In contrast, studies on tropical soil fauna have generally attributed a stronger role to rainfall and moisture (Burgess et al., 1999; Frith & Frith, 1990; Levings & Windsor, 1985; Pequeno et al., 2017; Wiwatwitaya & Takeda, 2005). These conclusions have limitations, for example, analyses which confound the effects of correlated variables, or biases induced by imperfect detection. That said, it is interesting that our results appeared more consistent with findings from temperate regions than from tropical forests. We suspect that the

often suggested effect of rainfall may actually reflect other factors, which can only be disentangled if analyzed jointly and with sufficient replication, as attempted here.

More generally, our results agree with the main conclusions from meta-analyses of hundreds of density time series from vertebrates and insects. Using a linearized Gompertz model accounting for measurement error, c ranged approximately from −1 (very strong density dependence) to 1 (no density dependence) across species, but was typically closer to 1 (Knape & de Valpine, 2012). Our estimate of density dependence for *R. ovulum* (c = 0.87; 95%CI: 0.798 to 0.947) does not differ significantly from these figures. Remarkably, and contrary to our hypothesis, our estimate does not point to strong density dependence in tropical soil microarthropods, as could be expected from the strong competition with microbial decomposers and from the low density of soil microarthropods compared to temperate soils (Takeda & Abe, 2001). Further, addition of climate covariates to population models often contributes little to their predictive power (Knape & De Valpine, 2011). Accordingly, environmental effects accounted for a relatively small fraction of the variance in *pgr* (R^2 = 0.25). In this light, our results strengthen the conclusion that population dynamics often have a deterministic component, but stochastic processes can be at least as important.

Our analysis has some caveats. First, our data are limited to a single year, although seasonal patterns in soil fauna density appear to be consistent across years in tropical forests (Wiwatwitaya & Takeda, 2005). Second, our data do not account for juveniles. Species identification of immatures is currently impractical for most oribatid mites; even when identification is feasible, extraction efficiency from soil samples may differ between immatures and adults, for example, immatures may be more prone to desiccation or occur in a microhabitat different from that of adults (Norton & Ermilov, 2014). Therefore, accounting for further life stages will probably require models even more complex than the one developed here. Nonetheless, the effect of intraspecific competition is often stronger in juvenile stages (White, 2008). Likewise, juvenile oribatid mites are less resistant to desiccation than adults (Jalil, 1972) and thus are probably more impacted by thermal effects. Thus, omission of immatures is more likely to underestimate than to overestimate the effects observed here. Lastly, overestimation of detection probability in valleys (Figure S1) suggests that differences in density and its dynamics are even smaller than they appeared to be after correcting for imperfect detection (Figure 1a). However, we did not find any significant difference in *pgr* between habitats (Figure 2d), so our main findings are unlikely to be significantly biased because of this.

This study provides insight into the neglected population dynamics of soil animals. Using state-space modeling, we showed that the intra-annual population dynamics of the soil mite *R. ovulum* were density dependent in the studied tropical rain forest, albeit to a low degree. Further, *pgr* increased with resource supply (litterfall) but mainly decreased with maximum temperature. Because these environmental factors correlate somewhat over the year, there was a trade-off between food supply and thermal suitability, so that

the highest population growth occurred when neither factor was optimal for growth. Overall, our results suggest that similar mechanisms—namely density dependence and temperature—may shape the dynamics of soil animal populations across latitudes.

DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHOR CONTRIBUTION

PACLP involved in conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing the original draft, and writing—review and editing. EF involved in conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, and writing—review and editing. RAN involved in conceptualization, supervision, and writing—review and editing.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare, at https://doi.org/10.6084/m9.figshare.10193594.v2 (Pequeno, Franklin, & Norton, 2019).

REFERENCES

Adis, J., & Junk, W. J. (2002). Terrestrial invertebrates inhabiting lowland river floodplains of Central Amazonia and Central Europe: A review. *Freshwater Biology*, *47*(4), 711–731. https://doi.org/10.1046/j.1365-2427.2002.00892.x

Andre, H. M., Ducarme, X., & Lebrun, P. (2002). Soil biodiversity: myth, reality or conning? *Oikos*, *96*(1), 3–24. https://doi.org/10.1034/j.1600-0706.2002.11216.x

Ashford, O. S., Foster, W. A., Turner, B. L., Sayer, E. J., Sutcliffe, L., & Tanner, E. V. J. (2013). Litter manipulation and the soil arthropod community in a lowland tropical rainforest. *Soil Biology and Biochemistry*, *62*, 5–12. https://doi.org/10.1016/j.soilbio.2013.03.001

Auger-Méthé, M., Field, C., Albertsen, C. M., Derocher, A. E., Lewis, M. A., Jonsen, I. D., & Mills Flemming, J. (2016). State-space models' dirty little secrets: Even simple linear Gaussian models can have estimation problems. *Scientific Reports*, *6*, 26677. https://doi.org/10.1038/srep26677

Balogh, J., & Balogh, P. (1990). *Oribatid mites of the Neotropical region II*. Budapest, Hungary: Akadémiai Kiadó.

Beck, L. (1969). Zum jahreszeitlichen massenwechsel zweier oribatidenarten (Acari) imneotropischen Überschwemmungswald. *Verhandlungen der Deutschen Zoologischen Gesellschaft 32*: 535–540.

Bellier, E., Kéry, M., & Schaub, M. (2016). Simulation-based assessment of dynamic N-mixture models in the presence of density dependence and environmental stochasticity. *Methods in Ecology and Evolution*, *7*(9), 1029–1040. https://doi.org/10.1111/2041-210X.12572

Betini, G. S., Griswold, C. K., & Norris, D. R. (2013). Carry-over effects, sequential density dependence and the dynamics of populations in a seasonal environment. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1759), 20130110. https://doi.org/10.1098/rspb.2013.0110

Breheny, P., & Burchett, W. (2017). Visualization of regression models using visreg. *The R Journal*, *9*(2), 1–15. https://doi.org/10.32614/RJ-2017-046

Brown, G. P., & Shine, A. R. (2006). Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. *Ecology*, *87*(1), 133–143.

Burgess, N. D., Ponder, K. L., & Goddard, J. (1999). Surface and leaf-litter arthropods in the coastal forests of Tanzania. *African Journal of Ecology*, *37*, 355–365. https://doi.org/10.1046/j.1365-2028.1999.00188.x

Caldararu, S., Palmer, P. I., & Purves, D. W. (2012). Inferring Amazon leaf demography from satellite observations of leaf area index. *Biogeosciences*, *9*(4), 1389–1405. https://doi.org/10.5194/bg-9-1389-2012

Castilho, C. V., Magnusson, W. E., de Araújo, R. N. O., Luizão, R. C. C., Luizão, F. J., Lima, A. P., & Higuchi, N. (2006). Variation in aboveground tree live biomass in a central Amazonian Forest: Effects of soil and topography. *Forest Ecology and Management*, *234*(1–3), 85–96. https://doi.org/10.1016/j.foreco.2006.06.024

Choi, W. I., Moorhead, D. L., Neher, D. A., & Ryoo, M. I. (2006). A modeling study of soil temperature and moisture effects on population dynamics of *Paronychiurus kimi* (Collembola: Onychiuridae). *Biology and Fertility of Soils*, *43*(1), 69–75. https://doi.org/10.1007/s00374-005-0062-5

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, *8*(3), 224–228. https://doi.org/10.1038/s41558-018-0067-3

Conceição, A. C. (2017). *Análise multi-anial da dinâmica de preodução de serapilheira fina em uma floresta da Amazônia central*. Manaus, Brazil: Instituto Nacional de Pesquisas da Amazônia.

Dail, D., & Madsen, L. (2011). Models for estimating abundance from repeated counts of an open metapopulation. *Biometrics*, *67*(2), 577–587. https://doi.org/10.1111/j.1541-0420.2010.01465.x

de Moraes, J., Franklin, E., Morais, J., & de Souza, J. L. P. (2011). Species diversity of edaphic mites (Acari: Oribatida) and effects of topography, soil properties and litter gradients on their qualitative and quantitative composition in 64 km2 of forest in Amazonia. *Experimental & Applied Acarology*, *55*, 39–63. https://doi.org/10.1007/s10493-011-9451-7

Dennis, B., Ponciano, J. M., Lele, S. R., Taper, M. L., & Staples, D. F. (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*, *76*(3), 323–341. https://doi.org/10.1890/0012-9615(2006)76[323:EDDPNA]2.0.CO;2

Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C., & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, *105*(18), 6668–6672. https://doi.org/10.1073/pnas.0709472105

Dunham, K., & Grand, J. B. (2016). Effects of model complexity and priors on estimation using sequential importance sampling/resampling for species conservation. *Ecological Modelling*, *340*, 28–36. https://doi.org/10.1016/j.ecolmodel.2016.08.010

Ferguson, S. H., & Joly, D. O. (2002). Dynamics of springtail and mite populations: The role of density dependence, predation,

and weather. *Ecological Entomology*, 27(5), 565–573. https://doi.org/10.1046/j.1365-2311.2002.00441.x

Franklin, E., & de Morais, J. W. (2006). Soil mesofauna in central Amazon. In F. M. S. Moreira, J. O. Siqueira & L. Brussaard (Eds.), *Soil biodiversity in Amazonian and other Brazilian ecosystems* (pp. 142–162). Oxfordshire, UK: CABI Publishing. https://doi.org/10.1079/9781845930325.0142

Frith, D., & Frith, C. (1990). Invertebrate seasonality of litter populations in an Australian upland tropical rain forest. *Biotropica*, 22(2), 181–190.

García-Carreras, B., & Reuman, D. C. (2011). An empirical link between the spectral colour of climate and the spectral colour of field populations in the context of climate change. *Journal of Animal Ecology*, 80(5), 1042–1048. https://doi.org/10.1111/j.1365-2656.2011.01833.x

Gillman, L. N., Wright, S. D., Cusens, J., Mcbride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, 24(1), 107–117. https://doi.org/10.1111/geb.12245

Herrando-Pèrez, S., Delean, S., Brook, B. W., & Bradshaw, C. J. A. (2012). Strength of density feedback in census data increases from slow to fast life histories. *Ecology and Evolution*, 2(8), 1922–1934. https://doi.org/10.1002/ece3.298

Herrando-Pérez, S., Delean, S., Brook, B. W., Cassey, P., & Bradshaw, C. J. A. (2014). Spatial climate patterns explain negligible variation in strength of compensatory density feedbacks in birds and mammals. *PLoS ONE*, 9(3), e91536. https://doi.org/10.1371/journal.pone.0091536

Hodnett, M. G., Vendrame, I., Filho, A. D. O. M., Oyama, M. D., & Tomasella, J. (1997). Soil water storage and groundwater behaviour in a catenary sequence beneath forest in central Amazonia: I. Comparisons between plateau, slope and valley floor. *Hydrology and Earty System Sciences*, 1(2), 265–277.

Hostetler, J. A., & Chandler, R. B. (2015). Improved state-space models for inference about spatial and temporal variation in abundance from count data. *Ecology*, 96(6), 1713–1723. https://doi.org/10.1890/14-1487.1

Illig, J., Langel, R., Norton, R. A., Scheu, S., & Maraun, M. (2005). Where are the decomposers? Uncovering the soil food web of a tropical montane rain forest in southern Ecuador using stable isotopes (15N). *Journal of Tropical Ecology*, 21(5), 589–593. https://doi.org/10.1017/S0266467405002646

Jalil, M. (1972). The effect of desiccation on some oribatid mites. *Proceedings of the Entomological Society of Washington*, 74(4), 406–410.

Karels, T. J., & Boonstra, R. (2000). Concurrent density dependence and independence in populations. *Nature Letters*, 408, 460–463.

Kingsolver, J. G., Diamond, S. E., & Buckley, L. B. (2013). Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Functional Ecology*, 27(6), 1415–1423. https://doi.org/10.1111/1365-2435.12145

Knape, J., & De Valpine, P. (2011). Effects of weather and climate on the dynamics of animal population time series. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 278(1708), 985–992. https://doi.org/10.1098/rspb.2010.1333

Knape, J., & de Valpine, P. (2012). Are patterns of density dependence in the Global Population Dynamics Database driven by uncertainty about population abundance? *Ecology Letters*, 15(1), 17–23. https://doi.org/10.1111/j.1461-0248.2011.01702.x

Kuznetsova, N. A. (2007). Long-term dynamics of Collembolan populations in forest and meadow ecosystems. *Entomological Review*, 87(1), 11–24. https://doi.org/10.1134/s0013873807010022

Lebreton, J.-D., & Gimenez, O. (2013). Detecting and estimating density dependence in wildlife populations. *The Journal of Wildlife Management*, 77(1), 12–23. https://doi.org/10.1002/jwmg.425

Levings, S. C., & Windsor, D. M. (1984). Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica*, 16(2), 125–131. https://doi.org/10.2307/2387844

Levings, S. C., & Windsor, D. M. (1985). Litter arthropod populations in a tropical deciduous forest: Relationships between years and arthropod groups. *Journal of Animal Ecology*, 54(1), 61–69. https://doi.org/10.2307/4620

Luizão, R. C. C., Luizão, F. J., Paiva, R. Q., Monteiro, T. F., Sousa, L. S., & Kruijt, B. (2004). Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest. *Global Change Biology*, 10(5), 592–600. https://doi.org/10.1111/j.1529-8817.2003.00757.x

MacNally, R. (2000). Regression and model-building in conservation biology, biogeography and ecology: The distinction between – and reconciliation of – 'predictive' and 'explanatory' models RALPHMAC. *Biodiversity and Conservation*, 9, 655–671. https://doi.org/10.1023/A

Marra, P. P., Cohen, E. B., Scott, L. R., Rutter, J. E., & Christopher, T. M. (2015). A call for full annual cycle research in animal ecology. *Biology Letters*, 11(8), 1–4. https://doi.org/10.1098/rsbl.2015.0552

Martius, C., Höfer, H., Garcia, M. V. B., Jörg, R., Förster, B., & Hanagarth, W. (2004). Microclimate in agroforestry systems in central Amazonia: Does canopy closure matter to soil organisms? *Agrogorestry Systems*, 60, 291–304. https://doi.org/10.1023/B

Norton, R. O. Y. A., & Ermilov, S. G. (2014). Catalogue and historical overview of juvenile instars of oribatid mites (Acari: Oribatida). *Zootaxa*, 3833(1), 1–132.

Pequeno, P. A. C. L., & Franklin, E. (2014). What drives the dynamics of a soil mite population under seasonal flooding? A null model analysis. *Experimental & Applied Acarology*, 62(2), 215–224. https://doi.org/10.1007/s10493-013-9731-5

Pequeno, P. A. C. L., Franklin, E., & Norton, R. A. (2019). Data from: Determinants of intra-annual population dynamics in a tropical soil arthropod. figshare. https://doi.org/10.6084/m9.figshare.10193594.v2

Pequeno, P. A. C. L., Franklin, E., Norton, R. A., & De Morais, J. W. (2018). A tropical arthropod unravels local and global environmental dependence of seasonal temperature–size response. *Biology Letters*, 14, 1–4. https://doi.org/10.1098/rsbl.2018.0125

Pequeno, P. A. C. L., Franklin, E., Norton, R., de Morais, J., & Guilherme, D. (2017). Spatial abundance pattern of a common soil arthropod changes suddenly with season in a tropical rainforest. *Pedobiologia*, 63, 46–51. https://doi.org/10.1016/j.pedobi.2017.07.002

Peschel, K., Norton, R., Scheu, S., & Maraun, M. (2006). Do oribatid mites live in enemy-free space? Evidence from feeding experiments with the predatory mite *Pergamasus septentrionalis*. *Soil Biology and Biochemistry*, 38(9), 2985–2989. https://doi.org/10.1016/j.soilbio.2006.04.035

Pfingstl, T. (2013). Population dynamics of intertidal oribatid mites (Acari: Cryptostigmata) from the subtropical archipelago of Bermuda. *Experimental and Applied Acarology*, 61(2), 161–172. https://doi.org/10.1007/s10493-013-9687-5

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd international workshop on distributed statistical computing.

R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Sayer, E. J. (2006). Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, 81(1), 1–31. https://doi.org/10.1017/S1464793105006846

Sibly, R. M., & Hone, J. (2002). Population growth rate and its determinants: An overview. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1425), 1153–1170. https://doi.org/10.1098/rstb.2002.1117

Stamou, G. P., & Sgardelis, S. P. (1989). Seasonal distribution patterns of oribatid mites (Acari: Cryptostigmata) in a forest ecosystem. *Journal of Animal Ecology*, 58(3), 893–904. https://doi.org/10.2307/5131

Stamou, G. P., Stamou, G. V., Papatheodorou, E. M., Argyropoulou, M. D., & Tzafestas, S. G. (2004). Population dynamics and life history tactics of arthropods from Mediterranean-type ecosystems. *Oikos*, 104, 98–108. https://doi.org/10.1111/j.0030-1299.2004.12382.x

Takeda, H., & Abe, T. (2001). Templates of food-habitat resources for the organization of soil animals in temperate and tropical forests. *Ecological Research*, 16(5), 961–973. https://doi.org/10.1046/j.1440-1703.2001.00450.x

Van Der Geest, L. P. S., Elliot, S. L., Breeuwer, J. A. J., & Beerling, E. A. M. (2000). Diseases of mites. *Experimental and Applied Acarology*, 24, 497–560. https://doi.org/10.1023/A:1026518418163

Wagner, F. H., Hérault, B., Rossi, V., Hilker, T., Maeda, E. E., Sanchez, A., … Aragão, L. E. O. C. (2017). Climate drivers of the Amazon forest greening. *PLoS ONE*, 12(7), 1–15. https://doi.org/10.1371/journal.pone.0180932

White, T. C. R. (2008). The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*, 83(3), 227–248. https://doi.org/10.1111/j.1469-185X.2008.00041.x

Wilson, E. O. (2005). Oribatid mite predation by small ants of the genus Pheidole. *Insectes Sociaux*, 52(3), 263–265. https://doi.org/10.1007/s00040-005-0802-4

Wiwatwitaya, D., & Takeda, H. (2005). Seasonal changes in soil arthropod abundance in the dry evergreen forest of north-east Thailand, with special reference to collembolan communities. *Ecological Research*, 20(1), 59–70. https://doi.org/10.1007/s11284-004-0013-x

Yu-Sung, S., & Yajima, M. (2015). R2jags: using R to run JAGS. Retrieved from https://cran.r-project.org/package=R2jags

Zanchi, F. B., Meesters, A. G. C. A., Waterloo, M. J., Kruijt, B., Kesselmeier, J., Luizão, F. J., & Dolman, A. J. (2014). Soil CO2 exchange in seven pristine Amazonian rain forest sites in relation to soil temperature. *Agricultural and Forest Meteorology*, 192–193, 96–107. https://doi.org/10.1016/j.agrformet.2014.03.009

Ziebarth, N. L., Abbott, K. C., & Ives, A. R. (2010). Weak population regulation in ecological time series. *Ecology Letters*, 13(1), 21–31. https://doi.org/10.1111/j.1461-0248.2009.01393.x

Zuur, A., Ieno E., Walker N., Saveliev A., and Smith G. (2009). *Mixed Effects Models and Extensions in Ecology with R*, p. 574. New York, NY: Springer.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.