Authors for correspondence:
Greg P. A. Lamarre
e-mail: greglamarre973@gmail.com
Nicholas A. Pardikes
e-mail: nickpardikes@gmail.com

†These authors contributed equally to the paper.

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More winners than losers over 12 years of monitoring tiger moths (Erebidae: Arctiinae) on Barro Colorado Island, Panama

Greg P. A. Lamarre[1,2,7,†], Nicholas A. Pardikes[1,3,†], Simon Segar[4], Charles N. Hackforth[5], Michel Laguerre[6], Benoît Vincent[6], Yacksecari Lopez[7], Filonila Perez[7], Ricardo Bobadilla[7], José Alejandro Ramírez Silva[7] and Yves Basset[1,2,7,8]

[1]Department of Ecology, Institute of Entomology, Biology Centre, Czech Academy of Sciences, Ceske Budejovice 37005, Czech Republic
[2]Faculty of Sciences, University of South Bohemia, Ceske Budejovice, Czech Republic
[3]Department of Life and Earth Sciences, Perimeter College, Georgia State University, Atlanta, USA
[4]Agriculture and Environment Department, Harper Adams University, Newport, Shropshire TF10 8NB, UK
[5]Department of Geography, University College London, Gower Street, London WC1E 6BT, UK
[6]Muséum National d'Histoire Naturelle, Département Systématique et Évolution, Entomologie, 57 rue Cuvier, Paris, France
[7]ForestGEO, Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panamá City, Republic of Panamá
[8]Maestria de Entomologia, Universidad de Panamá, Apartado 3366, Panamá 4, Panamá

GPAL, 0000-0002-7645-985X; NAP, 0000-0002-9175-4494; SS, 0000-0001-6621-9409; BV, 0000-0002-2515-2284; YB, 0000-0002-1942-5717

Understanding the causes and consequences of insect declines has become an important goal in ecology, particularly in the tropics, where most terrestrial diversity exists. Over the past 12 years, the ForestGEO Arthropod Initiative has systematically monitored multiple insect groups on Barro Colorado Island (BCI), Panama, providing baseline data for assessing long-term population trends. Here, we estimate the rates of change in abundance among 96 tiger moth species on BCI. Population trends of most species were stable ($n = 20$) or increasing ($n = 62$), with few ($n = 14$) declining species. Our analysis of morphological and climatic sensitivity traits associated with population trends shows that species-specific responses to climate were most strongly linked with trends. Specifically, tiger moth species that are more abundant in warmer and wetter years are more likely to show population increases. Our study contrasts with recent findings indicating insect decline in tropical and temperate regions. These results highlight the significant role of biotic responses to climate in determining long-term population trends and suggest that future climate changes are likely to impact tropical insect communities.

1. Introduction

Ongoing declines in insect biodiversity threaten to destabilize ecosystems worldwide [1]. Climate change and other threats affect insect population dynamics in temperate regions [2,3], but similar data are lacking in the species-rich tropics [4]. Tropical insects may be impacted by global mean temperatures and extreme climatic events. For example, many insect species shift their geographic range poleward or to higher elevations in response to increased mean temperatures [5–7]. Temperature changes may affect insect activity, development, phenology

and survival directly or indirectly through host phenological shifts or effects of temperature on plant chemistry [8]. Many tropical insects are extreme resource or microhabitat specialists and may be more susceptible to such changes [9,10]. Poikilothermic organisms cannot regulate their body temperature, and temperatures that exceed their thermal safety margin may thus result in significant fitness declines [11–14]. However, insect functional traits may be associated with potential declines in tropical communities, but the extent is unclear.

Tiger moths include contrasting tribes with high morphological and ecological variation [15]. They comprise generalists and specialist consumers, including the only known lineages capable of sequestrating secondary compounds from lichens, used to defend against predators and pathogens [16]. Arctiinae exhibit a wide range of wing colouration, lightness and size [17].

Such high inter-species variation may lead to divergent responses to climate change and help predict insect population dynamics in the face of climate change [18–20]. Here, we examine population trends among 96 tiger moth species over the past 12 years in Panama and test for their association with morphological and climatic sensitivity (e.g. sensitivity to mean monthly precipitation) traits and phylogenetic relatedness. Due to dispersal limitations, we predict that smaller wingspan moths may be more sensitive to climate changes [7]. However, larger species may be more prone to thermal exhaustion due to higher energy requirements [21,22]. We also predict that species with darker colouration may not favour increased solar radiation, particularly during the prolonged dry season [23,24]. Resource specialists such as lichen feeders are suspected to be particularly impacted by recent climate anomalies even if little data exist on lichen feeders in tropical regions. We predict that the effects of climatic sensitivity traits on temporal trends may depend on morphology.

2. Material and methods

(a) Study site and climate data
We performed this study on Barro Colorado Island (BCI) in Panama (9.15° N, 79.85° W; approximately 140 m elevation), a tropical lowland rainforest. The island is mainly preserved and covered by lowland tropical forests with few anthropogenic disturbances. BCI receives an average of 2662 mm rainfall per year and an annual average daily maximum and minimum air temperatures of 31°C and 23.6°C, respectively (see [25]).

(b) Arctiinae data and functional traits
Since March 2009, the ForestGEO Arthropod Initiative has monitored several insect groups, including Arctiinae, using a standardized approach. The protocol consists of automatic black-light traps installed in the forest understory at 10 sites [26]. The traps operate for two non-consecutive nights at each site during four surveys in March, May, September and November (total 80 trap-nights/year). The two non-consecutive sampling nights within each month were combined for this analysis. We accumulated 12 years of continuous monitoring for a total of 47 data points for each species (due to the pandemic, we missed one sample date). We also collated morphometry, phylogeny and functional traits for 188 Arctiinae species [27]. We argue that these functional traits are directly related to population density under an assumption of climate change. We also quantified species-specific sensitivity traits to several climatic variables, represented as beta coefficients extracted from a Bayesian negative binomial regression model run separately for each

species. Description of traits and predictors are provided in electronic supplementary material, S1 and S2. Each species was characterized with a unique DNA barcode, deposited in the public library BOLD [28].

(c) Data analysis
We restricted the statistical analysis to common species observed during at least 6 of the 12 study years to get more robust estimates of population trends [29]. This reduced the number of species from 188 to 96. To examine rates of change through time, we modelled the sum abundance of all 96 species together and moth species individually as a function of year. We accounted for seasonality by including month as a cofactor in all subsequent models. The extracted year coefficients served as the estimates of population trends through time. We also investigated how sensitive our results were to the period selected by removing the first and second years of sampling from our analyses. We used a Bayesian linear model and implemented continuous probabilities to provide a 'degree of belief' in population trends. We calculated the 'degree of belief' that the parameter for 'year' was greater than one or between specific values by counting the number of posterior draws that met our criteria and dividing that by the total number of posterior samples. We reported the number of species for whom the 'degree of belief' (probability) fell below 33.3% (i.e. 'decrease' category, twice as much confidence in a decrease than an increase), fell above 66.7% (i.e. 'increasing' category, twice as much confidence in an increase than a decrease) and the number of species whose degree of belief fell in between 33.3% and 66.7% per cent (i.e. 'stable' category, no strong evidence of increase or decrease). With quarterly abundance data for each species per year, the total abundance of moths and counts of each moth species were modelled as a negative binomial distribution with a logarithmic function. This distribution is appropriate for overdispersed count data, which was observed in many of our species. All models met assumptions of uniformity of residuals, autocorrelation and zero-inflation using simulated residuals from the DHARMa package [30]. Year coefficients from these models are on a logarithmic scale and can be interpreted directly or as multiplicative rates of change after being exponentiated. We calculated the mean, 95% and 80% credible intervals from each species' posterior probability distribution.

(d) Analysis of associations between traits and trends
After estimating population trends using Bayesian linear models, we examined associations between species traits (see [27]) and population trends using generalized least-squared (GLS) and phylogenetic generalized least-squared (PGLS) analyses using the nlme package in R [31]. We predicted population trends (extracted means of the posterior distributions as the estimates of change through time) as a function of a set of functional response traits, sensitivity to climate variables, or a combination of both using a GLS, with a Gaussian error distribution. All continuous predictors were mean-centred to improve interpretation and model performance. We also used a PGLS model with Brownian motion correlation among species to account for any phylogenetic signal in population trends. We tested for phylogenetic signal in the residuals of the GLS model using the R package *picante* [32]. All models included total abundance or the proportion of sample periods observed to account for differences in commonness and density among species. We checked and met model assumptions (normality of residuals, heteroscedasticity and autocorrelation) using simulated residuals from the DHARMa package [30]. We compared and evaluated GLS and PGLS model performances using AICc, root mean squared error (RMSE) and variance explained (R^2). We acknowledge the switch from Bayesian to frequentists paradigms; we use trends estimated with a reasonable degree of certainty and consider PGLS the most appropriate approach here.
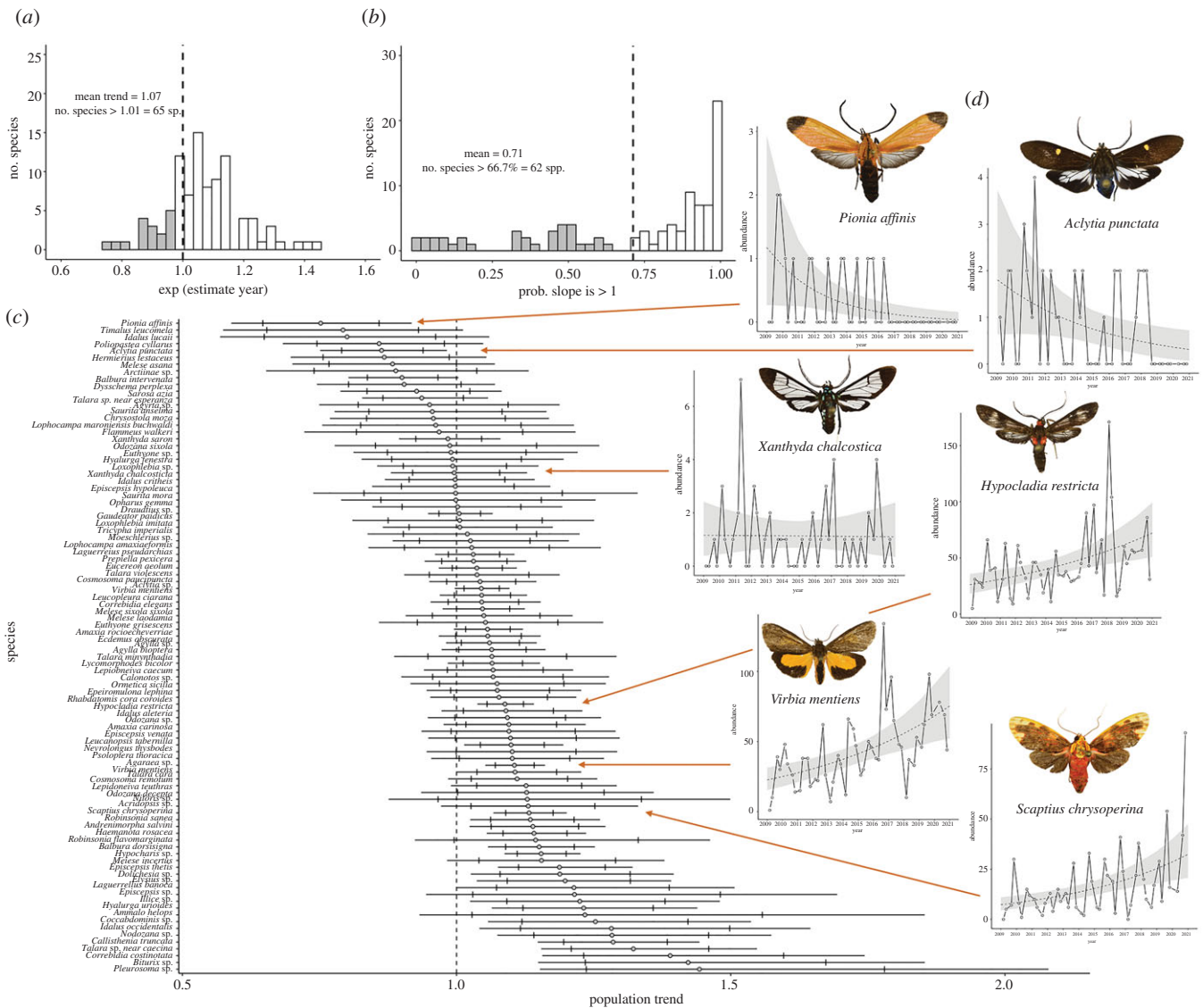
Figure 1. (*a*) Distribution of Arctiinae population trends over the 12 years from the negative binomial Bayesian regression. Shaded bars in the histogram represent estimates of population trends (mean of posterior distribution) that are less than 0.98, suggesting population declines. The dashed line denotes where trends are stable (e.g. exp(Neg. Binomial.Year.Coefficient) = 1). (*b*) The histogram displays the distribution of 'degree of belief' that exponentiated means of the posterior probability distribution were greater than one. This was calculated as the proportion of posterior draws for each species that were greater than one. (*c*) Estimates of population trends over the past 12 years among 96 Arctiinae species monitored on BCI. Each point represents the exponentiated mean of the posterior distribution from the negative binomial Bayesian regression for each species. The horizontal lines represent the 95% credible intervals, and the vertical lines display the 80% credible intervals. (*d*) Examples of the temporal dynamic of six commonly collected Arctiinae on BCI using abundance-based time-series (see electronic supplementary material, figure S4).

3. Results

(a) Population trends in Neotropical Arctiinae

Estimates of population trends in abundance over the past 12 years at BCI revealed that the entire tiger moth community had increased by 6% (95% CI: 1.01,1.11) per year (electronic supplementary material, figure S5). The probability that tiger moth abundance increased by at least 1% per year is 98%. Estimates of species-specific responses among tiger moth species revealed that most species (82 out of 96) were either stable or increased in abundance (figure 1). Sixty-two of the 96 species showed a strong degree of belief (greater than 66.7%) that their population trend was increasing (i.e. greater than one). Only 14 species showed strong evidence of declines (less than 33.3%) and the remaining 20 species did not have strong evidence of increased or decreased trends, suggesting stable dynamics. Removing 2009 or both 2009 and 2010 did not significantly alter the number of species present in each category mentioned above of

population trends (electronic supplementary material, figures S6 and S7; table S1). Of the 20 species whose trends were stable, the mean probability that their trend lies within ±1% per year was 10% (electronic supplementary material, figure S8). The high degree of uncertainty in these 20 'stable' species may be due to their low abundances across sample periods. They were commonly observed in our traps but were generally not abundant when sampled. For 16/20 species, the average number of individuals collected in each sample period (*n* = 48) was less than one. This suggests that their estimates of population trends are uncertain, and more data may be necessary to predict their trends more accurately.

(b) Association between species-specific traits and trends

Models that accounted for correlations in population trends among species (PGLS) generally explained more variance but showed consistently higher AICc values. There was no

Table 1. Results from the top GLS model (e.g. climate sensitivity) after AICc model selection. We indicate significant associations ($p < 0.05$) in italics. We modelled 93 species since three did not have genetic information and were not included in the PGLS. Standardized estimates and 95% confidence intervals are presented. CV abundance represents the coefficient of variation in abundance.

predictors	estimates	95% CI	p-value
intercept	*1.06*	*1.04–1.08*	*<0.001*
log(total abundance)	0.01	−0.02–0.04	0.635
CV abundance	−0.01	−0.04–0.02	0.513
maximum temperature	*0.04*	*0.02–0.07*	*0.002*
minimum temperature	*−0.03*	*−0.05–0.00*	*0.019*
average precipitation	*0.03*	*0.00–0.05*	*0.023*
geographic range	−0.02	−0.04–0.01	0.153
observations	93		
R^2 Nagelkerke	0.359		

phylogenetic signal in the residuals of any GLS models (electronic supplementary material, table S2). Table 1 shows a detailed model output for the top-performing physiological (e.g. climatic sensitivity). The climatic sensitivity model represented 91.2% of the AICc weight among all models. Morphological traits did not significantly predict changes in abundance over time and only explained 7% of the variation in population trends. The best combined morphological and climate sensitivity model explained 41% of the variation in population trends but was 4.7 AICc units below the best-performing physiological model. Our strongest predictors of population trends were variables measuring climatic sensitivity (table 1). A positive association existed between population trends and sensitivity to average monthly precipitation (figure 2a). Based on standardized beta coefficients, the strongest predictor of population trends was sensitivity to the average monthly maximum temperature (figure 2b), with a standardized coefficient of 0.04 (CI 95% 0.02–0.07), suggesting that moths that are more abundant during warmer years are more likely to show increasing population trends.

4. Discussion

Our results highlight the vital role of specific differences in climate sensitivity in explaining variation in population trends in this tropical moth community. We indicate that most species have either increased or remained temporally stable over the past 12 years but are likely to be further influenced by future climate changes in Panama. The increasing and stable population dynamics contrast with observed sharp declines in caterpillar density in Costa Rica [33,34]. Climate change may have been a driving force in the decrease observed in the Costa Rican studies, but other factors, such as land-use changes and agricultural practices, likely induced decline. Our survey on BCI, an isolated protected forest island, indicates that common tiger moths showed widespread increases and temporal population stability.

Although several species show strong evidence of decline (figure 1), the overall temporal stability in arctiine

populations highlights that insect declines are not homogeneous. Since more than 60% of tiger moth species have strong evidence of increasing in abundance since 2009, our results also contrast with other studies [33–35]. We hypothesize that this pattern may have important implications locally, with cascading impacts driven by herbivory and predation at higher trophic levels. Although it is well-established that climate change affects species distributions and abundances of insect herbivores [33,34,36], the impacts of climate change on trophic interactions have been less studied [10]. Outbreak species may benefit from climate changes, as reported for two Panamanian species [5]. In a previous study on BCI, we observed that populations of some large Saturniidae species are increasing [28]. We also showed that recent climate anomalies occurring in the tropics, such as increasing average precipitation on BCI [25], have significant and positive effects on the abundance of tiger moths (figure 2a). A similar trend has been observed in the United Kingdom [37] but is also likely driven by differential responses to land-use change. We expected that morphological traits relating to climate, especially thermal tolerance, would predict temporal trends. Our results contradict this expectation, and while phylogenetic information does increase the proportion of variance explained, this comes at a high cost in terms of model parameters. Hence, it is unlikely that any of the morphological traits that we measured may be significant predictors of response to climate, although we cannot rule out that such traits exist. Few studies have found that functional traits predict population trends [22,35].

Species-specific climate sensitivity traits were the best predictors of temporal trends of tiger moths on BCI. Sensitivity to average precipitation showed a significant and positive relationship with population trends. Species that were more abundant in months with higher precipitation showed positive population trends (figure 2). Sensitivity to average maximum temperatures also predicted temporal trends, indicating that population abundances of species that were twice as abundant in months with a one-degree increase in temperature have increased by 5% each year. Increased temperatures facilitate more frequent, longer or more effective territorial and mate-locating behaviours [38]. Prolonged exposure at extreme temperatures can also influence the pace of insect life cycles, thus affecting developmental time and population growth rates [39,40]. The inclusion of thermal tolerance measurements is primordial to correctly interpret moth population dynamics patterns [11–14]. Our analysis provides evidence of a stable and increasing tropical moth community. Still, it highlights the potential future impact of climate change, as climatic sensitivity traits were the best predictors of population trends. Since 1981, BCI has experienced a 17.9% increase in mean annual precipitation [19], and we showed that moth populations that respond to increasing precipitation in Panama are also increasing.

With increasing air temperature also predicted for tropical regions by recent models [41,42], this species group may indeed be favoured by future environmental conditions. However, future phenotypic responses and upper levels of thermal tolerance are hard to predict. Should the rate of warming exceed physiological response capacities, we can expect sharp declines in population density for many tropical insect species.
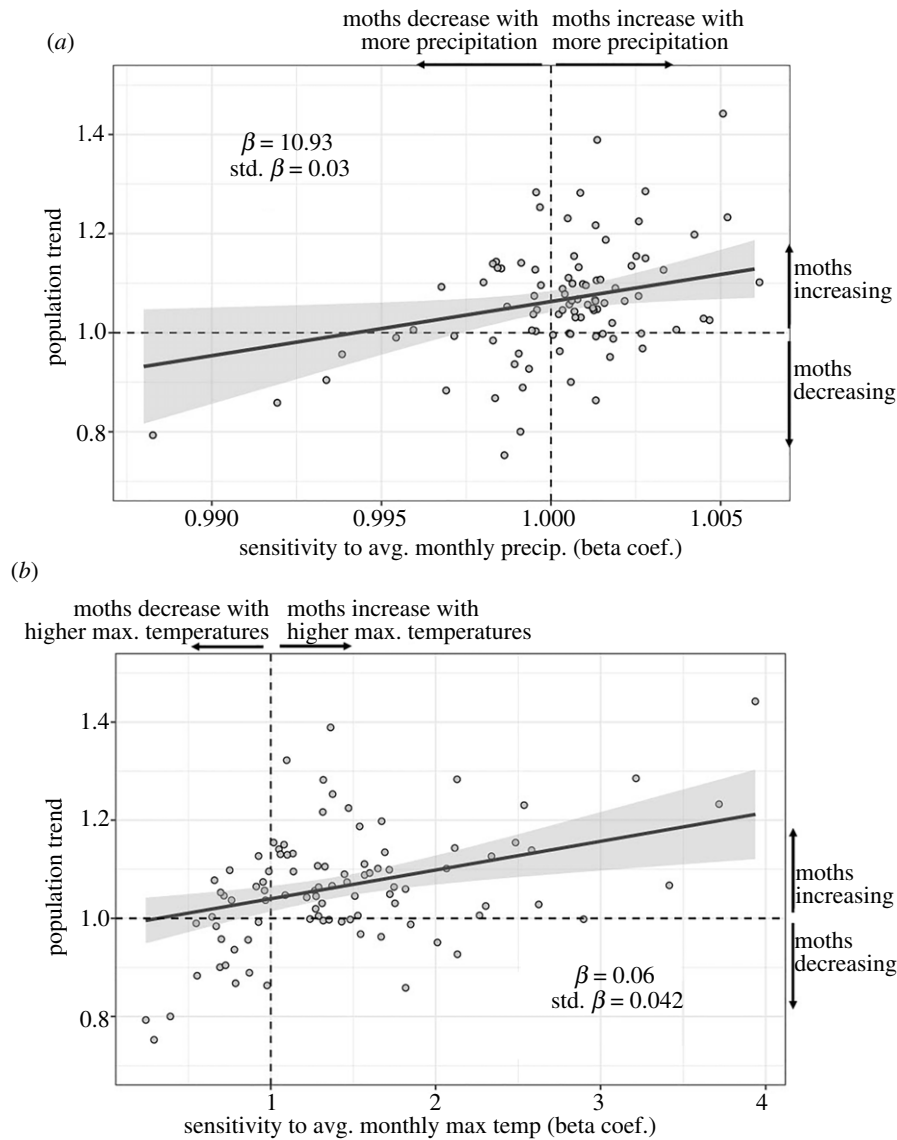
Figure 2. Exponentiated rates of change in Arctiinae abundance regressed against the exponentiated coefficients of (*a*) sensitivity to average monthly precipitation and (*b*) sensitivity to average maximum monthly temperatures. The fitted line and 95% confidence intervals are from multiple linear regression, and the raw and standardized beta coefficients are shown within each figure. The dashed horizontal and vertical lines at 1 for each axis represent coefficient values when there is no multiplicative change in trend over the years (*y*-axis) or no multiplicative change in abundance in response to either average precipitation or maximum temperature. A value of two (*x*-axis) suggests that species are twice as abundant in months with a 1°C increase in average monthly maximum temperature or a 1 mm increase in average monthly precipitation.

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