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

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

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Abstract: 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 last 12 years, the ForestGEO Arthropod Initiative has systematically monitored multiple insect groups on Barro Colorado Island, 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.

Keywords: climate change; functional traits; population trend; rainforest; Panama

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 coloration, 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 coloration may not favor 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 exists 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; ~140m 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 2,662mm 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 blacklight traps installed in the forest understory at ten 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 supplementary materials 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 at least 6 of the 12 study years to get more robust estimates of population trends [42]. This reduced the number of species from

88 188 to 96. To examine rates of change through time, we modeled the sum abundance of all 96
89 species together and moth species individually as a function of year. We accounted for seasonality
90 by including month as a cofactor in all subsequent models. The extracted year coefficients served
91 as the estimates of population trends through time. We also investigated how sensitive our results
92 were to the period selected by removing the first and second years of sampling from our analyses.
93 We used a Bayesian linear model and implemented continuous probabilities to provide a "degree
94 of belief" in population trends. We calculated the "degree of belief" that the parameter for "year"
95 was greater than one or between specific values by counting the number of posterior draws that
96 met our criteria and dividing that by the total number of posterior samples. We reported the number
97 of species for whom the "degree of belief" (probability) fell below 33.3% (i.e., "decrease" category,
98 twice as much confidence in a decrease than an increase), fell above 66.7% (i.e., "increasing"
99 category, twice as much confidence in an increase than a decrease), and the number of species
100 whose degree of belief fell in between 33.3% and 66.7% percent (i.e., "stable" category, no strong
101 evidence of increase or decrease). With quarterly abundance data for each species per year, the
102 total abundance of moths and counts of each moth species were modeled as a negative binomial
103 distribution with a logarithmic function. This distribution is appropriate for overdispersed count
104 data, which was observed in many of our species. All models met assumptions of uniformity of
105 residuals, autocorrelation, and zero-inflation using simulated residuals from the *DHARMa* package
106 [31]. Year coefficients from these models are on a logarithmic scale and can be interpreted directly
107 or as multiplicative rates of change after being exponentiated. We calculated the mean, 95%, and
108 80% credible intervals from each species' posterior probability distribution.
109

110 **(d) Analysis of associations between traits and trends**
111 After estimating population trends using Bayesian linear models, we examined associations
112 between species traits [see 27] and population trends using generalized least squared (GLS) and
113 phylogenetic generalized least squares (PGLS) analyses using the *nlme* package in R [29]. We
114 predicted population trends (extracted means of the posterior distributions as the estimates of
115 change through time) as a function of a set of functional response traits, sensitivity to climate
116 variables, or a combination of both using a GLS, with a Gaussian error distribution. All continuous
117 predictors were mean-centered to improve interpretation and model performance. We also used a
118 PGLS model with Brownian motion correlation among species to account for any phylogenetic
119 signal in population trends. We tested for phylogenetic signal in the residuals of the GLS model
120 using the R package *picante* [30]. All models included total abundance or the proportion of sample
121 periods observed to account for differences in commonness and density among species. We
122 checked and met model assumptions (normality of residuals, heteroscedasticity, and
123 autocorrelation) using simulated residuals from the *DHARMa* package [31]. We compared and
124 evaluated GLS and PGLS model performances using AICc, Root Mean Squared Error (RMSE),
125 and variance explained (R^2). We acknowledge the switch from Bayesian to frequentists paradigms;
126 we use trends estimated with a reasonable degree of certainty and consider PGLS the most
127 appropriate approach here.

3. RESULTS

(3-1) 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 (Fig. 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 (Fig. 1). The probability (degree of belief) of an increasing trend was strong (>66.7%) in 62 of the 96 species. Only fourteen species showed strong evidence of declines (<33.3%). The remaining twenty 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 (Fig. S6 & S7; Table S1). Of the twenty species whose trends were stable, the mean probability that their trend lies within ±1% per year was 10% (Fig. S8). We argue that the high degree of uncertainty in these twenty "stable" species is 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 abundance, across all 48 sample periods, was less than one. This suggests that their trend estimates are uncertain, and more data may be necessary to predict their trends more accurately.

(3-2) 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 phylogenetic signal in the residuals of any GLS models (Table S2). We provide a detailed model output for the top-performing physiological (e.g., climatic sensitivity) model in Table 1. The climatic sensitivity model represented 91.2% of the AICc weight among all models. No morphological traits significantly predicted trends and only explained 7% of the variation in population trends. The best combined morphological and climate sensitivity model explained 41% 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 (Fig. 2A). Based on standardized beta coefficients, the strongest predictor of population trends was sensitivity to the average monthly maximum temperature (Fig. 2B), with a standardized coefficient of 0.04 (CI 95% 0.02-0.07), suggesting that moths which 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

168 influenced by future climate changes in Panama. The increasing and stable population dynamics
169 contrast with observed sharp declines in caterpillar density in Costa Rica [33-34]. Climate change
170 may have been a driving force in the decrease observed in the Costa Rican studies, but other
171 factors, such as land-use changes and agricultural practices, likely induced decline. Our survey on
172 BCI, an isolated protected forest island, indicates that common tiger moths showed widespread
173 increases and temporal population stability.

174 Although several species show strong evidence of decline (Fig. 1), the overall temporal
175 stability in arctiine populations highlights that insect declines are not homogenous. Since more
176 than 60% of tiger moth species have strong evidence of increasing in abundance since 2009, our
177 results also contrast with other studies [33-35]. We hypothesize that this pattern may have
178 important implications locally, with cascading impacts driven by herbivory and predation at higher
179 trophic levels. Although it is well-established that climate change affects species distributions and
180 abundances of insect herbivores [32-34], the impacts of climate change on trophic interactions
181 have been less studied [10]. Outbreak species may benefit from climate changes, as reported for
182 two Panamanian species [5]. In a previous study on BCI, we observed that populations of some
183 large Saturniidae species are increasing [28]. We also showed that recent climate anomalies
184 occurring in the tropics, such as increasing average precipitation on BCI [25], have significant and
185 positive effects on the abundance of tiger moths (Fig. 2A). A similar trend has been observed in
186 the United Kingdom [36] but is also likely driven by differential responses to land-use change. We
187 expected that morphological traits relating to climate, especially thermal tolerance, would predict
188 temporal trends. Our results contradict this expectation, and while phylogenetic information does
189 increase the proportion of variance explained, this comes at a high cost in terms of model
190 parameters. Hence, it is unlikely that any of the morphological traits that we measured may be
191 significant predictors of response to climate, although we cannot rule out such traits exist. Few
192 studies have found that functional traits predict population trends [22,35].

193 Species-specific climate sensitivity traits were the best predictors of temporal trends of
194 tiger moths on BCI. Sensitivity to average precipitation showed a significant and positive
195 relationship with population trends. Species that were more abundant in months with higher
196 precipitation showed positive population trends (Fig. 2). Sensitivity to average maximum
197 temperatures also predicted temporal trends, indicating that population abundances of species that
198 were twice as abundant in months with a one-degree increase in temperature have increased by
199 5% each year. Increased temperatures facilitate more frequent, longer, or more effective territorial
200 and mate-locating behaviors [37]. Prolonged exposure at extreme temperatures can also influence
201 the pace of insect life cycles, thus affecting developmental time and population growth rates [38-
202 39]. The inclusion of thermal tolerance measurements is primordial to correctly interpret moth
203 population dynamics patterns [11-14]. Our analysis provides evidence of a stable and increasing
204 tropical moth community. Still, it highlights the potential future impact of climate change, as
205 climatic sensitivity traits were the best predictors of population trends. Since 1981 BCI has
206 experienced a 17.9% increase in mean annual precipitation [19], and we showed that moth
207 populations that respond to increasing precipitation in Panama are also increasing.

208 With increasing air temperature also predicted for tropical regions by recent models [40-41], this
209 species group may indeed be favored by future environmental conditions. However, future
210 phenotypic responses and upper levels of thermal tolerance are hard to predict. Should the rate of
211 warming exceed physiological response capacities, we can expect sharp declines in population
212 density for many tropical insect species.

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220 **Figure Captions**
221 **FIGURE 1**: A) Distribution of Arctiinae population trends over the 12 years from the negative
222 binomial Bayesian regression. Shaded bars in the histogram represent estimates of population
223 trends (mean of posterior distribution) that are less than 0.98, suggesting population declines. The
224 dotted line denotes where trends are stable (e.g., exp(Neg. Binomial.Year.Coefficient)= 1). B) The
225 histogram displays the distribution of "degree of belief" that exponentiated means of the posterior
226 probability distribution were greater than one. This was calculated as the proportion of posterior
227 draws for each species that were greater than one. C) Estimates of population trends over the last
228 12-years among 96 Arctiinae species monitored on BCI. Each point represents the exponentiated
229 mean of the posterior distribution from the Negative Binomial Bayesian regression for each
230 species. The horizontal lines represent the 95% credible intervals, and the vertical lines display the
231 80% credible intervals. D) Examples of the temporal dynamic of six commonly-collected Arctiinae
232 on BCI using abundance-based time-series.

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234 **FIGURE 2:** Exponentiated rates of change in Arctiinae abundance regressed against the
235 exponentiated coefficients of A) sensitivity to average monthly precipitation and B) sensitivity to
236 average maximum monthly temperatures. The fitted line and 95% confidence intervals are from
237 multiple linear regression, and the raw and standardized beta coefficients are shown within each
238 figure. The dotted horizontal and vertical lines at 1 for each axis represent coefficient values when
239 there is no multiplicative change in trend over the years (y-axis) or no multiplicative change in
240 abundance in response to either average precipitation or maximum temperature. A value of two
241 (x-axis) suggests that species are twice as abundant in months with a 1°C increase in average
242 monthly maximum temperature or a 1mm increase in average monthly precipitation.
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247 **TABLE 1:** Results from the top GLS model (e.g., climate sensitivity) after AICc model selection.
248 We indicate significant associations (P<0.05) in bold. We modeled 93 species since three did not
249 have genetic information and were not included in the PGLS. Standardized estimates and 95%
250 confidence intervals are presented. CV abundance represents the coefficient of variation in
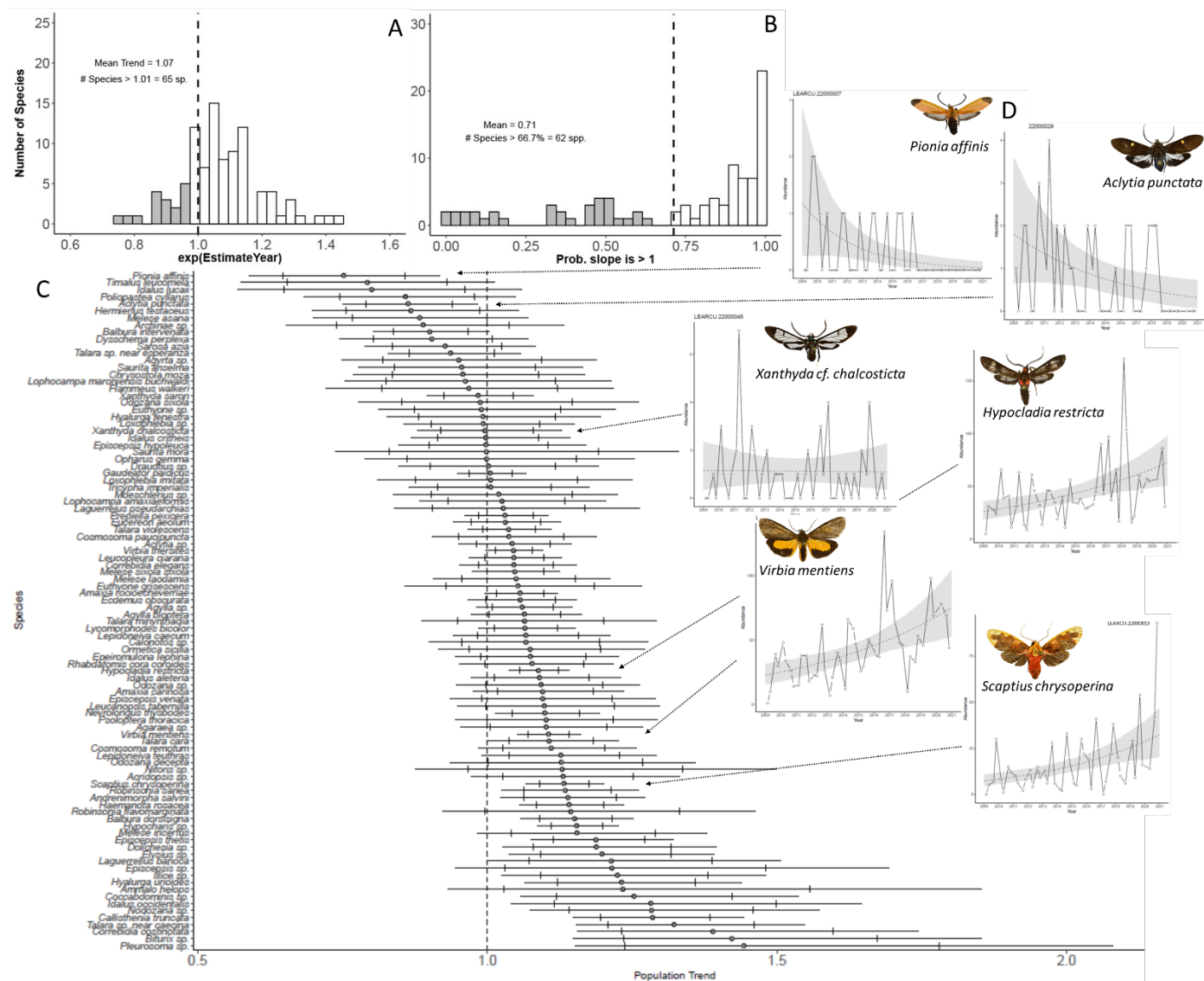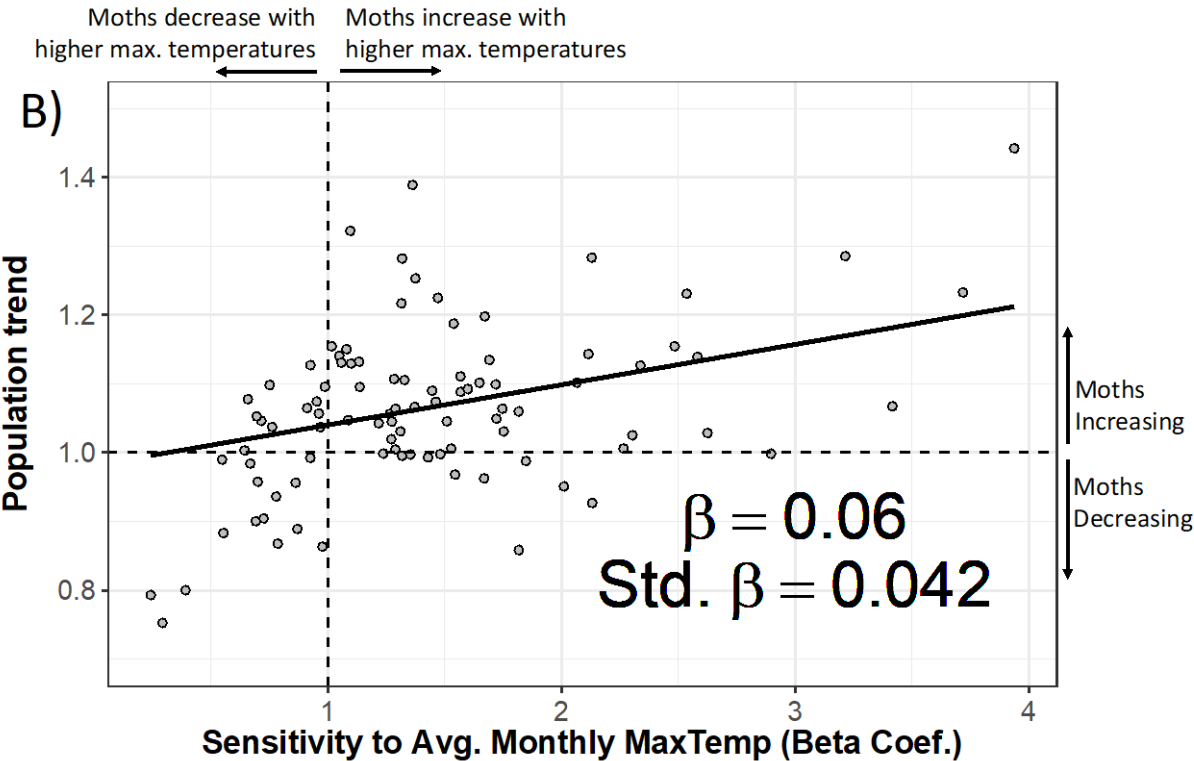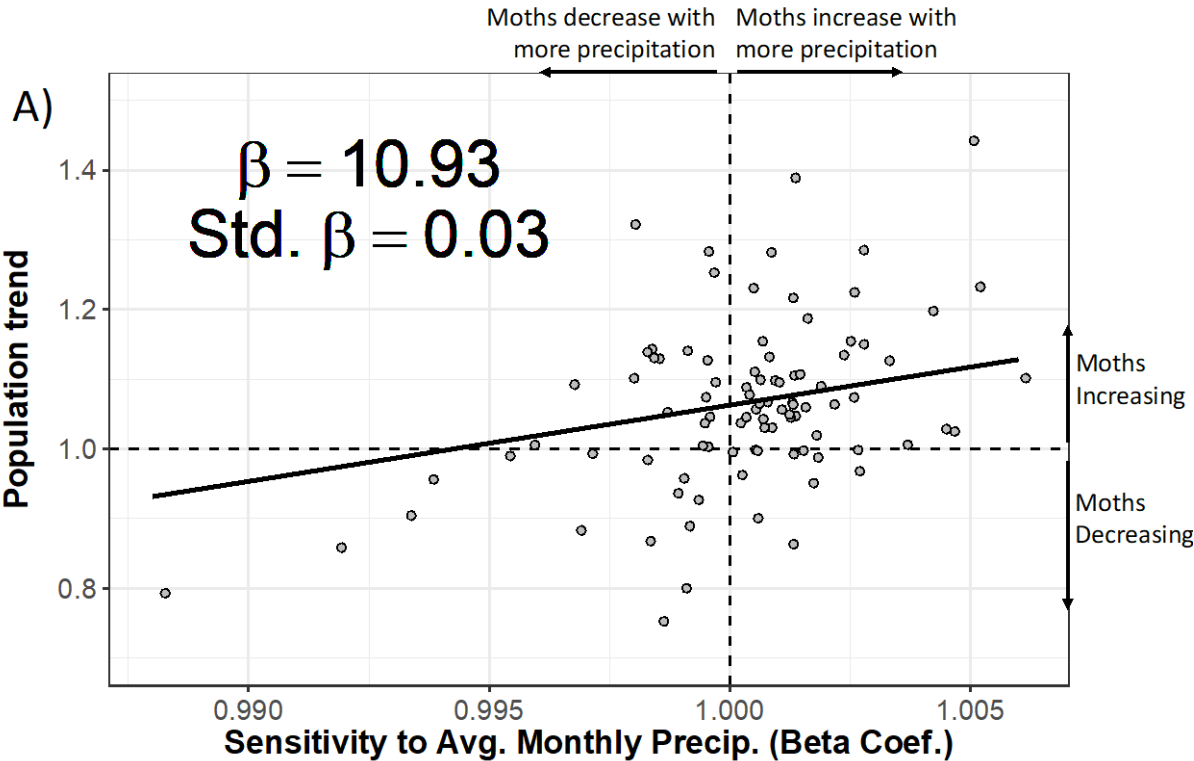251 abundance.

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FIGURE 1

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A)

Moths decrease with   Moths increase with
more precipitation   more precipitation

$\beta = 10.93$
Std. $\beta = 0.03$

Population trend

1.4

1.2

1.0

0.8

Moths
Increasing

Moths
Decreasing

0.990   0.995   1.000   1.005

Sensitivity to Avg. Monthly Precip. (Beta Coef.)

B)

Moths decrease with   Moths increase with
higher max. temperatures   higher max. temperatures

Population trend

1.4

1.2

1.0

0.8

$\beta = 0.06$
Std. $\beta = 0.042$

Moths
Increasing

Moths
Decreasing

1   2   3   4

Sensitivity to Avg. Monthly MaxTemp (Beta Coef.)

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TABLE 1
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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		

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