FORESTGEO ARTHROPOD INITIATIVE
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Program coordinator: Yves Basset, Smithsonian Tropical Research Institute (STRI), bassety@si.edu

I. BACKGROUND AND PARTICIPATING FORESTGEO SITES

The 'ForestGEO Arthropod Initiative' aims at monitoring key arthropod assemblages over long-term and studying insect-plant interactions over the network of the Forest Global Earth Observatories (ForestGEO, https://forestgeo.si.edu/research-programs/arthropod-initiative). The Initiative integrates with ongoing monitoring of plant dynamics within the ForestGEO network, causes minimum possible impact to the plots and focus on a priority set of assemblages chosen for their ecological relevance, taxonomic tractability and ease of sampling. At each participating ForestGEO site, the first years of the program are usually devoted to a 'baseline' survey. The baseline survey is followed by longer-term programs of field work and analysis, organized into two main sub-programs: monitoring, and key interaction studies. The monitoring sub-program is directed to detecting long-term changes, as reflected in priority assemblages, driven by climatic cycles, climatic change and landscape scale habitat alteration. Monitoring protocols are derived from those used during the baseline survey. The food web approach of interaction studies targets interactions between plants and specific insect assemblages, with different protocols than those used for monitoring.

Currently, the Arthropod Initiative involves seven ForestGEO sites: Yasuni in Ecuador, Barro Colorado Island (BCI) in Panama, Khao Chong (KHC) in Thailand, Tai Po Kau (Hong Kong), Dinghushan and Xishuangbanna (XTBG) in China and Wanang (WAN) in Papua New Guinea. At BCI, four full-time research assistants were in charge of arthropod monitoring protocols in 2022: Filonila Perez, Ricardo Bobadilla, Yacksecari Lopez and Alejandro Ramirez. The program coordinator, YB, doubled as BCI site supervisor. Greg Lamarre (University of South Bohemia) is research associate at STRI and collaborates on most projects based in Panama. The collections and staff of the ForestGEO Arthropod Initiative in Panama are based at the Tupper complex in Panama City.

The insect monitoring at KHC in 2022 was under the responsibility of Montarika Panmeng (Tim, lab leader, Plate I, item 2), Suthhatip Kongnakorn (Gift), Manat Reungaew (Jeen), Sontaya Promchaisri (Mos), Tassanai Kaewyod (Est) and, as recent staff, Nantakan Duangwang (Lip). Supervision at KHC was assured by Sarayudh Bunyavejchewin, Nantachai Pongpattananurak, (Kasetsart University, Bangkok), and YB, who worked at KHC for two weeks during November. At WAN, Francesca Dem (Binatang Research Centre), Vojtech Novotny (Czech Academy of Sciences and University of South Bohemia) and YB supervised assistants Roll Liplip, Ruma Umari, Fidelis Kimberg and Ananias Kamam, who were in charge of ForestGEO protocols.

II. TAXONOMIC STUDIES AND DNA BARCODING

David Donoso (Escuela Politécnica Nacional, Ecuador) continued working on BCI ants, which amount to nearly 400 species. Dimitri Forrero and Alejandro Ramirez improved the taxonomy of the reduviids of BCI. A shipment of arctiine moths was delivered to Michel Laguerre in France, who is revising their taxonomy and will describe new species from BCI. We are trying to organize the taxonomic study of several focal groups at Khao Chong and disseminate specimens at different institutions in Thailand. We also occasionally refined the identification of the specimens representing 14,000 insect sequences available in projects ABCI, AKHC and AWAN on the Barcode of Life (BOLD) platform. We started a large project on BCI funded by SENACYT, looking at insect diversity across 25 small plots of 20x20m (Plate I, items 5-8). Insect data are obtained via DNA metabarcoding and will be related to various variable accounting for forest structure and plant composition (ForestGEO data). This opened new collaborations with STRI scientists Joe Wright and Helene Muller-Landau (LIDAR and vegetation data) and with Jeremy DeWaard, Evgeny Zakharov and Kate Perez (DNA metabarcoding) at the University of Guelph, Canada, a leader in DNA metabarcoding. In 2022, we obtained insect samples with Malaise traps, Winkler samples and pitfall traps and processed about a third of planned samples. Preliminary results indicate that over 5,500 Barcode Index Numbers (species) have been recovered in these samples (Plate I, item 8). In 2023 we plan to obtain further insect samples from the plots with Berlese, beating, light traps and intercept-flight traps. The gigabytes of data related to this project are stored on the mBrave platform. Daniel Soutos-Vilarós (University of South Bohemia), research assistant Ana Cecilia Zamora and intern Yahir Campuzano are helping with the project. DNA metabarcoding should help us one day to efficiently monitor most of arthropod species on BCI and at other sites.

III. MONITORING: BARRO COLORADO ISLAND, KHAO CHONG AND WANANG

Year 2022 represented the fourteen year of insect monitoring at BCI. So far, the BCI database contains data on 687,642 arthropods, including 2,420 focal species (1,776 of which with pictures, 73%) and 75,219 pinned specimens in our collections (275 drawers). Each year we collect at BCI 330 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 40 bee bait samples) and in 2022 this represented 28,021 arthropods. Francisco Serrano and

Alejandro Ramirez are nearing submission of their MSc theses on the passalid beetles and reduviid bugs of BCI, respectively. Esme Ashe-Jepson from Cambridge University in UK is finished with field work and is writing several manuscripts on butterfly thermal tolerance in collaboration with Greg Lamarre and Benita Laird-Hopkins (University of South Bohemia). Ernesto Bonadies (PhD student) and Daniel Soutos-Vilarós (both University of South Bohemia) are studying the genome of common insect pollinators on BCI. All field data have been collected and preliminary results are interesting (Plate I, item 9). Eduardo Navarro-Valencia, intern at STRI, helped by volunteer Ana Sofia Santos, is modeling the abundance, species richness, functional diversity and phylogenetic diversity over time of geometrid moths on BCI (Plate I, item 10). See Eduardo's enthusiastic ForestGEO blog at https://forestgeo.si.edu/blog/spotlight-series-eduardo-navarro-valencia-arthropods-barro-colorado-island. In 2022, analyses of monitoring and functional data from BCI focused mostly on pollinators, geometrid moths, ants, and other social insects (Plate I, items 11-12). Greg Lamarre and colleagues published in *Biological Letters* an analysis of recent trends for arctiine moth populations on BCI. Few species are declining, and we reproduce the integrality of the article in Appendix I.

2022 represented our twelfth year of monitoring at KHC. We collected 370 insect samples (80 light trap samples, 50 Winkler samples, 120 butterfly transects, 40 termite transects and 80 McPhail samples). So far, our database includes 261,347 specimens (37,511 pinned specimens in collections) and 2,544 focal species. We still need to improve on processing quickly insect samples and including representative insect pictures in our database. At WAN, 2022 represented the tenth year of insect monitoring (Plate I, items 3-4). The ForestGEO insect database contains data on 87,000 specimens, but apart from butterflies and fruit flies, few of these specimens are yet identified. A backlog of databasing data will be absorbed in 2023.

YB has participated to the project LOT (Life on Trees) in Peru, lead by Maurice Leponce (Royal Institute of Natural Sciences, Brussels, Belgium). The project aims at surveying most Eukaryotes supported by large rainforest trees.

IV. INTERACTION STUDIES

We are still in the process of analyzing data resulting from the study of seed predators and herbivore damage on seedlings at the three sites of BCI, KHC and WAN. These studies were funded by the Grant Agency of the Czech Republic and result from a collaboration with Sofia Gripenberg (University of Reading), Owen Lewis (University of Oxford), Richard Ctvrtecka; Philip Butterill, Leonardo Ré Jorge (University of South Bohemia) and Simon Segar (Harper Adams University). The final phase of this project monitored the survivorship of seedlings in control plots and in plots treated with insecticide, to evaluate the action of insect herbivores on seedlings. Richard Ctvrtecka is helping YB to database all the results and our seedling damage database includes 4.7 million records. We are still measuring herbivory data at KHC and expect to start analyzing these impressive data soon. The project "Integrating genomic and trophic information into long-term monitoring of tropical insects: pollinators on Barro Colorado Island, Panama" (Ernesto Bonadies, Daniel Souto-Vilarós, Greg Lamarre and YB) is progressing well with now all field data collected. The first analytical data are available (Plate I, item 9) and Ernesto presented preliminary results at the 2022 meeting of the British Ecological Society.

V. FORESTGEO ARTHROPOD DATABASE AND WEB SITES

Phil Butterill (University of South Bohemia) maintains the ForestGEO Arthropod database. We plan to include the insect seed predator data (see above) in the main database. These data represent over 80,000 insect records with hostplant information. The current list of web sites related to the ForestGEO Arthropod Initiative includes:

- https://fgeoarthropods.si.edu/ : public (with registration) web version of the ForestGEO Arthropod database, mirroring snapshots of data for the sites of BCI, YAS, KHC and WAN.
- https://forestgeo.si.edu/research-programs/arthropod-initiative : ForestGEO site, including protocols, annual reports and interactive taxonomic keys.
- https://striresearch.si.edu/yves-basset-lab/ : research activities of YB and collaborators.

The database and related web pages will allow to foster scientific collaboration via a better visibility of the ForestGEO Arthropod Initiative.

VI. SCIENTIFIC OUTPUT

In 2022, the ForestGEO Arthropod Initiative trained, at the sites of BCI, KHC and WAN, 15 assistants (5: BCI, 6: KHC, 4: WAN); 2 interns (BCI); two MSc student (BCI) and one PhD students (BCI). The following talks in relation with the ForestGEO Arthropod Initiative were presented at international meetings in 2022:

- Eduardo Navarro Valencia *et al*.: Geometridae of Barro Colorado Island: Can phylogenetic signal reveal responses to climate change? Youth Systematic Forum 2022, 11 November 2022, https://systass.org/events/future-events/ysf2022/

- Daniel Souto-Vilarós *et al*.: Monitoring tropical arthropods in Barro Colorado Island, Panama, using DNA metabarcoding. International Conference on DNA Barcoding and Biodiversity, Sofia, Bulgaria. May 25 – 27, 2022. https://cmebg.com/en/sabitia/icdbb2022/
- Yves Basset: co-organizer of the symposium on "Insect decline: temperature versus tropical trends", part of the INTECOL (The International Association for Ecology) meeting in Geneva, Switzerland (one day long, 15 talks), 28 August - 2 September 2022. https://intecol2021.org/ (Plate I, item 1).
- Ernesto Bonadies *et al* "Population trends of tropical insect pollinators after 10-years of monitoring on Barro Colorado Island, Panama", EKOLOGIE 2022, 8th Conference of the Czech Society for Ecology, 7-9 September 2022, https://www.cspe.cz/en/konference/ekologie-2022/. "Tropical insect pollinators in a changing world", British Ecological Society Meeting 2022, Edinburgh, Scotland, 18-21 September 2022, https://www.britishecologicalsociety.org/events/bes-annual-meeting-2022/

Collectively, we wrote 6 publications in 2022, and many manuscripts are in preparation (see below). We are starting new collaborations in the field of DNA metabarcoding and bioacoustics monitoring which should lead to an increasing number of exciting publications.

Publications related to the ForestGEO Arthropod Initiative in 2022:

Basset, Y., Blažek, P., Souto-Vilarós, D., Vargas, G., Ramírez Silva, J.A., Barrios, H., Perez, F., Bobadilla, R., Lopez, Y., Ctvrtecka, R., Šípek, P., Solís, A., Segar, S.T. & Lamarre, G.P.A. 2022. Towards a functional classification of poorly known tropical insects: The case of rhinoceros beetles (Coleoptera, Dynastinae) in Panama. *Insect Conservation and Diversity*, in press.

Basset, Y., Hajibabaei, M., Wright, M.T.G., Castillo, A.M., Donoso, D.A., Segar, S.T., Souto-Vilarós, D. Soliman, D.Y., Roslin, T., Smith, M.A., Lamarre, G.P.A., De León, L.F., Decaëns, T., Palacios-Vargas, J.G., Castaño-Meneses, G., Scheffrahn, R.H., Rivera, M., Perez, F., Bobadilla, R., Lopez, Y., Ramirez Silva, J.A., Montejo Cruz, M., Arango Galván, A. & Barrios, H. (2022). Comparison of traditional and DNA metabarcoding samples for monitoring tropical soil arthropods (Formicidae, Collembola and Isoptera). *Scientific Reports*, **12**, 10762.

Donkersley, P., Ashton, L., Lamarre, G. P. A., & Segar, S. (2022) Global insect decline is the result of willful political failure: A battle plan for entomology. *Ecology and Evolution*, **12**, e9417.

Donoso, D.A., Basset, Y., Shik, J.Z., Forrister, D.L., Uquillas, A., Salazar Méndez , Y., Arizala, S., Polanco, P., Beckett, S., Dominguez G., D. & Barrios, H. 2022. Male ant reproductive investment in a seasonal wet tropical forest: consequences of future climate change. *PLoS ONE*, **17**, e0266222.

Harvey, J.A., Tougeron, K., Gols, R., …, Basset, Y., …, Lamarre, G.P.A., …, & Chown, S.L. 2022. Scientists' warning on climate change and insects. *Ecological Monographs*, in press.

Lamarre, G.P.A., Pardikes, N.A., Segar, S., Hackforth, C.N., Laguerre, M., Vincent, B., Lopez, Y., Perez, F., Bobadilla, R., Ramírez Silva, J.A**.,** Basset, Y. 2022. More winners than losers over 12 years of monitoring tiger moths (Erebidae: Arctiinae) on Barro Colorado Island, Panama. *Biology Letters*, **18**, 20210519.

Selected manuscripts in preparation related to the ForestGEO Arthropod Initiative:

Functional classification of Neotropical tiger moths (Erebidae-Arctiinae) provides insight on patterns of expected vulnerability to climate change (submitted to *Functional Ecology*)

Long-term monitoring of social insects in tropical rainforests (submitted to *Ecological Indicators*).

Calibrating biodiversity for long-term monitoring: detecting changes in assemblage composition from temporarily and spatially variable insect data.

Long term dynamics of a male ant assemblage in a tropical forest.

The magnitude of cryptic insect diversity in one tropical rainforest.

A comparison of the buffering ability of tropical and temperate butterflies.

Monitoring tropical arthropods in Barro Colorado Island, Panama, using DNA metabarcoding.

Plate I. Representative activities/items for the ForestGEO Arthropod Initiative in 2022. (1) Advertising flier for the symposium on insect decline at the 2022 INTECOL meeting in Geneva. (2) Tim (in green shirt) briefing students at Khao Chong. (3) Fruit flies (*Bactrocera* spp.) collected at baits in Wanang. (4) Ananias setting up Winklers at Wanang. (5) 25 Malaise traps drying up at STRI as part of the DNA metabarcoding project on BCI. (6) Yahir and Ana Cecilia setting up a Malaise trap on BCI for the DNA metabarcoding project. (7) LIDAR image of one of the 25 plots delineated on BCI for the DNA metabarcoding project. (8) Preliminary results of the DNA metabarcoding project on BCI: distribution of the number of Barcode Index Numbers among the 25 plots with (inset) the distribution of sequence length. So far, a third of the planned samples have recovered +5,500 arthropod BINs (species). (9) Preliminary results reporting genetic changes of BCI pollinators over time (E. Bonadies *et al.*, unpubl. data). (10) Local phylogenetic tree for BCI Geometridae (E. Navarro-Valencia *et al.*, unpubl. data). (11) Modeling the abundance and species richness of Passalidae over time (Basset *et al.*, submitted). (12) *Uranophora albiplaga*, one of the many arctiine moth species studied by Lamarre *et al.* (2022) on BCI (see full text below).

APPENDIX I. FULL TEXT OF LAMARRE *ET AL.* 2022 (see next page).

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Research

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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.

A contribution to the special feature 'Insect Decline' organised by Martin Gossner, Florian Menzel and Nadja Simons.

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THE ROYAL SOCIETY PUBLISHING

Global change biology

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 blacklight 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.
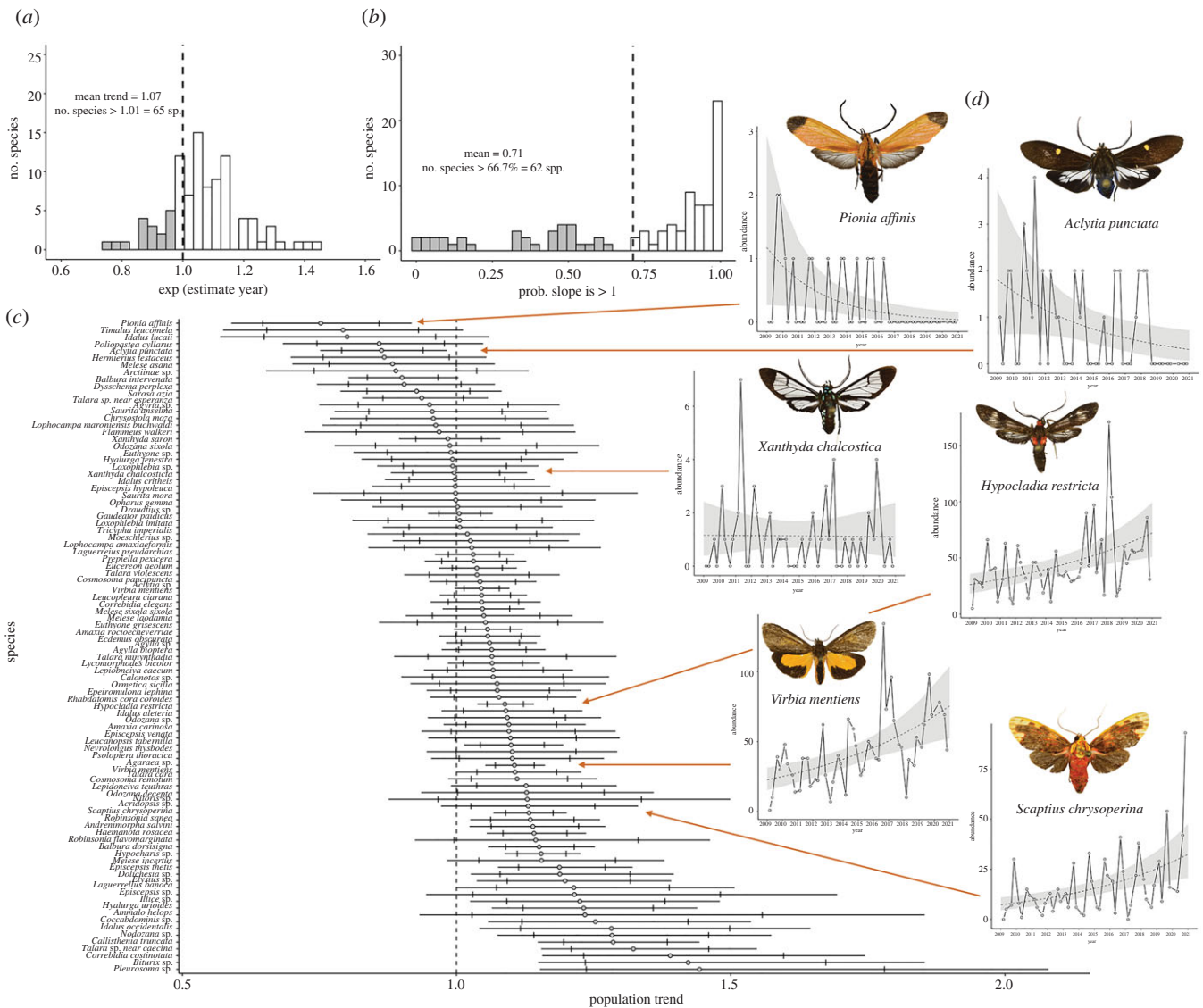
Figure 1. (*a*) Distribution of Arctiinae population trends over the 12 years from the negative binomial Bayesian regression. Shaded bars in the histogram represent estimates of population trends (mean of posterior distribution) that are less than 0.98, suggesting population declines. The dashed line 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.
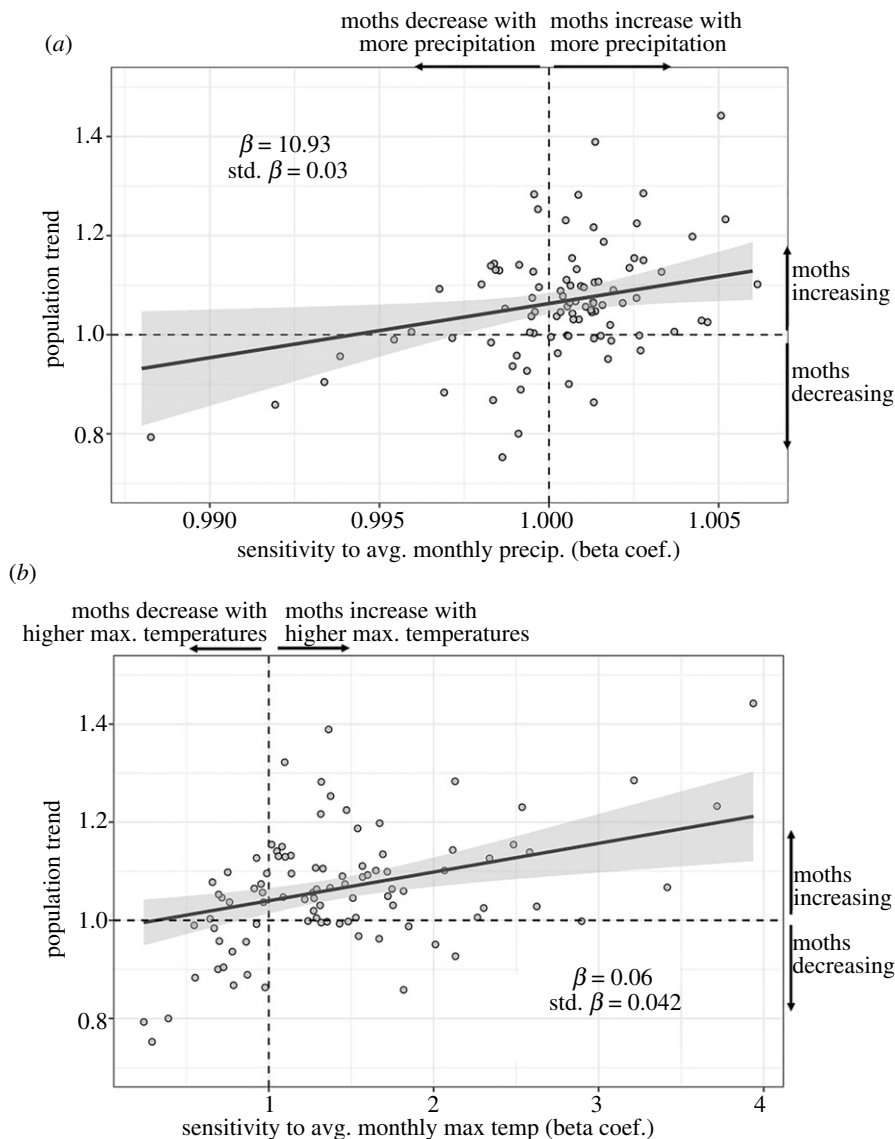
Figure 2. Exponentiated rates of change in Arctiinae abundance regressed against the exponentiated coefficients of (*a*) sensitivity to average monthly precipitation and (*b*) sensitivity to average maximum monthly temperatures. The fitted line and 95% confidence intervals are from multiple linear regression, 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.

References

1. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. 2014 Defaunation in the Anthropocene. Science 345, 401–406. (doi:10.1126/science.1251817)

2. Sánchez-Bayo F, Wyckhuys KAG. 2019 Worldwide decline of the entomofauna: a review of its drivers. Biol. Conserv. 232, 8–27. (doi:10.1016/j.biocon.2019.01.020)

3. Wagner DL, Fox R, Salcido DM, Dyer LA. 2021 A window to the world of global insect declines: Moth biodiversity trends are complex and heterogeneous. Proc. Natl Acad. Sci. USA 118, e2002549117. (doi:10.1073/pnas.2002549117)

4. Basset Y, Lamarre GPA. 2019 Toward a world that values insects. Science 364, 1230–1231. (doi:10.1126/science.aaw7071)

5. Van Bael S, Aiello A, Valderrama A, Medianero E, Samaniego M, Wright JS. 2004 General herbivore outbreak following an El Niño-related drought in a lowland Panamanian forest. J. Trop. Ecol. 20, 625–633. (doi:10.1017/S0266467404001725)

6. Battisti A, Stastny M, Netherer S, Robinet C, Schopf A, Roques A, Larsson S. 2005 Expansion of geographic range in the pine processionary moth caused by increased winter temperatures. Ecol. Appl. 15, 2084–2096. (doi:10.1890/04-1903)

7. Sekar S. 2012 A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? J. Anim. Ecol. 81, 174–184. (doi:10.1111/j.1365-2656.2011.01909.x)

8. Detto M, Wright JS, Calderon O, Muller-Landau H. 2018 Resource acquisition and reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation. Nature Comm. 9, 913. (doi:10.1038/s41467-018-03306-9)

9. Eggleton P. 2020 The state of the World's insects. Annu. Rev. Environ. Resour. 45, 61–82. (doi:10.1146/annurev-environ-012420-050035)

10. Schleuning M et al. 2020 Trait-based assessments of climate-change impacts on interacting species. Trends Ecol. Evol. 35, 319–328. (doi:10.1016/j.tree.2019.12.010)

11. Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008 Impacts of climate warming on terrestrial ectotherms across latitude. Proc. Natl Acad. Sci. USA 105, 6668–6672. (doi:10.1073/pnas.0709472105)

12. Kaspari M, Clay NA, Lucas J, Yanoviak SP, Kay A. 2015 Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. Glob. Chang. Biol. 21, 1092–1102. (doi:10.1111/gcb.12750)

13. García-Robledo C, Kuprewicz EK, Staines CL, Erwin TL, Kress WJ. 2016 Limited tolerance by insects to high temperatures across tropical elevational gradients and the implications of global warming for extinction. Proc. Natl Acad. Sci. USA 113, 680–685. (doi:10.1073/pnas.1507681113)

14. Pincebourde S, Casas J. 2019 Narrow safety margin in the phyllosphere during thermal extremes. Proc. Natl Acad. Sci. USA 116, 588–596. (doi:10.1073/pnas.1815828116)

15. Zenker M, Wahlberg N, Brehm G, Teston JA, Przybylowicz L, Pie MR, Freitas AV. 2017 Systematics and origin of moths in the subfamily Arctiinae (Lepidoptera, Erebidae) in the Neotropical región. Zool. Scripta 46, 348–362. (doi:10.1111/zsc.12202)

16. Chialvo SCH, Holland JD, Anderson TJ, Breinholt JW, Kawahara ZX, Liu S, Zaspel JM. 2018 A phylogenomic analysis of lichen-feeding tiger moths uncovers evolutionary origins of host chemical sequestration. Mol. Phylogenetics Evol. 121, 23–34. (doi:10.1016/j.ympev.2017.12.015)

17. Gawne R, Nijhout HF. 2020 The Arctiid Archetype: a new Lepidopteran Groundplan. Front. Ecol. Evol. 8, 175. (doi:10.3389/fevo.2020.00175)

18. Parmesan C. 2006 Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. Syst. 37, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)

19. Lavorel S et al. 2013 A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. J. Veg. Sci. 24, 942–948. (doi:10.1111/jvs.12083)

20. Kissling WD et al. 2018 Towards global data products of essential biodiversity variables on species traits. Nat. Ecol. Evol. 2, 1531–1540. (doi:10.1038/s41559-018-0667-3)

21. Slade EM, Merckx T, Riutta T, Bebber DP, Redhead D, Riordan P, Macdonald DW. 2013 Life-history traits and landscape characteristics predict macro-moth responses to forest fragmentation. Ecology 94, 1519–1530. (doi:10.1890/12-1366.1)

22. Coulthard E, Norrey J, Shortall C, Harris EW. 2019 Ecological traits predict population changes in moths. Biol. Conserv. 233, 213–219. (doi:10.1016/j.biocon.2019.02.023)

23. Heidrich L, Friess N, Fiedler K, Brandle M, Hausmann A, Brandl R, Zeuss D. 2018 The dark side of Lepidoptera: colour lightness of geometrid moths decreases with increasing latitude. Glob. Ecol. Biogeogr. 8, 1–10. (doi:10.1111/geb.12703)

24. Clusella-Trullas S, Nielsen M. 2020 The evolution of insect body coloration under changing climates. Curr. Opin. Insect. Sci. 41, 25–32. (doi:10.1016/j.cois.2020.05.007)

25. Anderson-Teixeira KJ et al. 2015 CTFS ForestGEO: a worldwide network monitoring forests in an era of global change. Glob. Chang. Biol. 21, 528–549. (doi:10.1111/gcb.12712)

26. Lucas M, Forero D, Basset Y. 2016 Diversity and recent population trends of assassin bugs (Hemiptera: Reduviidae) on Barro Colorado Island, Panama. Insect Conserv. Divers. 9, 546–558. (doi:10.1111/icad.12191)

27. Hackforth CN et al. In preparation. Functional classification of Neotropical tiger moths (Erebidae-Arctiinae) provides insight on vulnerability to climate change. Manuscript in preparation for Funct. Ecol.

28. Basset Y et al. 2017 The Saturniidae of Barro Colorado Island, Panama: a model taxon for studying the long-term effects of climate change? Ecol. Evol. 7, 1–14. (doi:10.1002/ece3.3515)

29. Lamarre GPA et al. 2022 Data from: More winners than losers over 12 years of monitoring tiger moths (Erebidae: Arctiinae) on Barro Colorado Island, Panama. FigShare. See https://smithsonian.figshare.com/articles/dataset/More_winners_than_losers_over_12_years_of_monitoring_tiger_moths_Erebidae_Arctiinae_on_Barro_Colorado_Island_Panama/16850218.

30. Hartig F. 2019 DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.2.4.

31. Pinheiro J, Bates D, DebRoy S, Sarkar D, Heisterkamp, S, Van Willigen B, Maintainer R. 2017 Package 'nlme'. Linear and nonlinear mixed effects models, version, 3(1).

32. Kembel S, Cowan P, Helmus M, Cornwell W, Morlon H, Ackerly D, Blomberg S, Webb C. 2010 Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26, 1463–1464. (doi:10.1093/bioinformatics/btq166)

33. Salcido DM, Forister ML, Garcia Lopez H, Dyer LA. 2020 Loss of dominant caterpillar genera in a protected tropical forest. Sci. Rep. 10, 422. (doi:10.1038/s41598-019-57226-9)

34. Janzen DH, Hallwachs W. 2021 To us insectometers, it is clear that insect decline in our Costa Rican tropics is real, so let's be kind to the survivors. Proc. Natl Acad. Sci. USA 118, e2002546117. (doi:10.1073/pnas.2002546117)

35. Forister ML et al. 2021 Fewer butterflies seen by community scientists across the warming and drying landscapes of the American West. Science 371, 1042–1045. (doi:10.1126/science.abe5585)

36. Fox J et al. 2012 Package 'car', p. 16. Vienna, Austria: R Foundation for Statistical Computing.

37. Fox R et al. 2021 The state of Britain's larger moths 2021. Wareham, UK: Butterfly Conservation, Rothamsted Research and UK Centre for Ecology & Hydrology. See https://butterfly-conservation.org/sites/default/files/2021-03/StateofMothsReport2021.pdf.

38. Hayes MP, Hitchcock GE, Knock RI, Lucas CBH, Tuerner EC. 2019 Temperature and territoriality in the Duke of Burgundy butterfly, Hamearis lucina. J.

Ins. Cons. **23**, 739–750. (doi:10.1007/s10841-019-00166-6)

39. Rebaudo F, Rabhi VB. 2018 Modeling temperature-dependent development rate and phenology in insects: review of major developments, challenges, and future directions. *Entom. Exp. Appl.* **166**, 607–617. (doi:10.1111/eea.12693)

40. Iltis C, Louapre P, Pecharova K, Thiery D, Zito S, Bois B, Moreau J. 2019 Are life-history traits equally affected by global warming? A case study combining a multi-trait approach with fine-grain climate modeling. *J. Ins. Physiol.* **117**, 103916. (doi:10.1016/j.jinsphys.2019.103916)

41. IPCC. 2021 Climate change 2021: the physical science basis. *Contribution of working group I to the sixth assessment report of the Intergovernmental Panel on Climate Change* (eds V. Masson-Delmotte et al.). Cambridge, UK: Cambridge University Press. See https://www.ipcc.ch/report/ar6/wg1/#FullReport.

42. Stocker T et al. 2014 Climate change 2013: the physical science basis. *Contribution of working group I to the fifth assessment report of the Intergovernmental Panel on Climate Change.* Cambridge, UK: Cambridge University Press. See https://www.ipcc.ch/report/ar5/wg1/.

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