

Global predation pressure redistribution under future climate change

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How climate affects biotic interactions is a question of urgent concern^{1–3}. Theory predicts that biotic interactions are stronger at lower latitudes^{4–6}. However, the role of climate in governing these patterns is typically assumed, rather than explicitly tested. Here, we dissected the influence of climatic descriptors on predation pressure using data from a global experiment with model caterpillars. We then used projections of future climate change to predict shifts in predation pressure. Climate, particularly components of temperature, explained latitudinal and elevational patterns of predation better than latitude or elevation by themselves. Projected predation pressure was greater under higher temperatures and more stable climates. Increased climatic instability projected for the near future predicts a general decrease in predation pressure over time. By identifying the current climatic drivers of global patterns in a key biotic interaction, we show how shifts in these drivers could alter the functioning of terrestrial ecosystems and their associated services.

Human activities are impacting the Earth's climate at an unprecedented rate⁷. Climate warming, temperature instability and extreme precipitation events are all increasing in intensity^{8,9}. These climate changes can alter the frequency, direction and magnitude of biotic interactions², and result in major biodiversity loss through the collapse of such interactions^{3,10}. Efforts to successfully manage and restore the ecosystems may be futile without a clearer understanding of the influence of accelerating climate change on the strength and frequency of biotic interactions^{2,3}.

Many types of biotic interactions tend to be stronger and more frequent towards lower latitudes^{6,11–14} (but see ref. ¹⁵) and elevations^{11,14}. These global (latitude) and local or regional (elevation) patterns indicate that climatic conditions may be a common driver underlying the strength and frequency of biotic interactions. However, previous macroecological studies of latitudinal and elevational gradients in biotic interactions (Fig. 1a) do not directly test the effect of climatic variables^{16,17}. Moreover, climatic conditions do not always correlate with changes in latitudinal and elevational gradients^{18,19}—a mismatch that can lead to spurious relationships between latitude and/or elevation, and biological responses²⁰. Large-scale patterns are typically inferred from a set of experiments and observations that vary in their methods and protocols²¹, thus

muddling climatic signatures. In contrast, standardized experiments replicated across regional and global scales allow us to separate the direct effects of climate from indirect effects of latitude or elevation on biotic interactions.

We explicitly tested whether and how key climate variables predict latitudinal and elevation patterns of predation pressure using a global dataset with model caterpillars¹⁴. Following a standardized protocol, this experiment recorded attack rates (over 12,694 caterpillar days) by arthropod, mammal and bird predators, across a 11,660 km latitudinal gradient (30.4° S to 74.3° N) and elevations spanning from 0 to 2,100 above sea level. We focused our analyses on attacks by arthropods alone, since previous results showed that global gradients in overall attack rates were driven by variation in arthropod predation¹⁴. As a response, we used the probability of a model caterpillar being attacked by an arthropod predator per day exposed¹⁴ (here, defined as the predation pressure). To separate the effects of climate from those of latitude and elevation, we extracted a set of bioclimatic and topographic variables from WorldClim version 2 and ENVIREM, at 1 km² resolution, for each of the 31 target sites included in the original experiment¹⁴ (see Methods). We then applied structural equation modelling (SEM) to determine the relative importance of the direct and indirect effects of absolute latitude, elevation and the underlying local climate on predation pressure. To derive succinct descriptors of climatic variation in multivariate space, we derived separate projections of temperature (first axis of a principal component analysis (PCA) including four components all representing different aspects of temperature) and precipitation (first axis of a PCA including five components all representing different aspects of precipitation) (Methods).

There was a strong positive effect of temperature variables ($\beta = 0.67$, s.e. = 0.21, $P < 0.001$) on attack rate (Fig. 1b), but no effect of precipitation ($\beta = 0.22$, s.e. = 0.20, $P = 0.28$). This analysis identifies temperature as the key climate driver of attack rates along the global latitudinal and elevation gradients. Because elevation and absolute latitude are negatively correlated with temperature components, they alter predation pressure indirectly through effects on temperature (Fig. 1b). The bioclimatic variables that comprised the components of temperature in the PCA included mean annual temperature (bio1), mean diurnal range (bio2), temperature seasonality (bio4) and temperature annual range (bio7) (Supplementary Table 1

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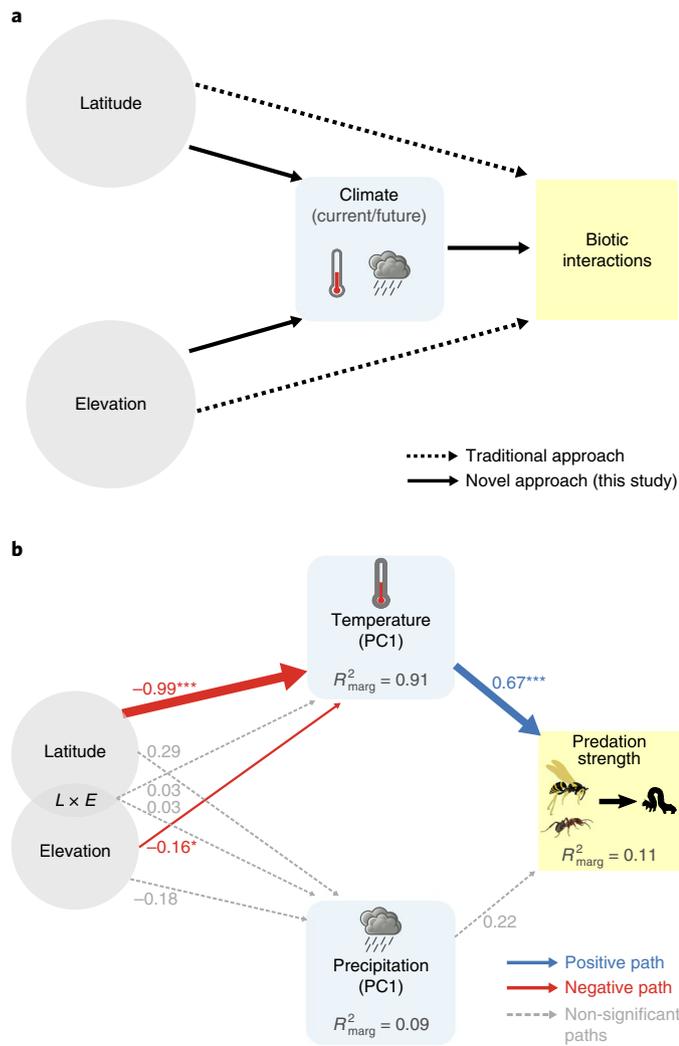


Fig. 1 | Direct and indirect effects of latitude, elevation and climate (current and future) on predation pressure. a, Conceptual representation of the traditional approach to understanding latitudinal and elevation patterns in the distribution of biotic interactions, in contrast with the new approach adopted here, where we identify the causal direct and indirect influence of latitude and elevation, and the underlying impact of climate on biotic interactions. **b**, Outcome of SEM showing the causal effects of latitude (L), elevation (E) and their interactions ($L \times E$) on individual components of temperature and precipitation (PC1), and on arthropod attack rates on model prey (data from ref. ¹⁴). Red, blue and grey lines represent negative, positive and non-significant adjusted paths of a piecewise SEM, respectively, with marginal R^2 values for endogenous variables. * $P < 0.05$, *** $P < 0.001$. Model fit: Fisher's $C = 10.3$, d.f. = 8, $P = 0.25$, small-sample-size corrected Akaike information criterion (AICc) = 53.9.

and Methods). The first PCA axis was driven by positive values of bio1 and negative values of bio4 and bio7 (Supplementary Table 1 and Supplementary Fig. 1); positive values of bio4 and bio7 represent sites with more stable temperature, as characterized by less variation within years. Therefore, the positive effect of temperature detected in our structural equation model indicates that predation pressure increases with mean annual temperature, and in climates with higher temperature stability. None of the topographical variables significantly altered arthropod attack rates (Supplementary Fig. 2), and their removal improved the description of the predation patterns (change in small-sample-size corrected Akaike information criterion, $\Delta\text{AICc} = 3.8$; Fig. 1b and Supplementary Fig. 2).

We provide strong empirical evidence that the current climate (and especially its temperature components) is the key determinant of latitudinal and elevational patterns in arthropod predation across the globe. Any changes to current climatic conditions could then alter the distribution of predation pressure at the global scale. To evaluate the extent to which current patterns in predator–prey interactions and predation pressure may shift with ongoing climate change, we applied two complementary analytical approaches: (1) generalized linear mixed-effects modelling (GLMM), which projected predation pressure at a local scale over time (years 2050 and 2070), and (2) ecological niche modelling (ENM), which projected predation pressure over time and space (that is, 2050 and 2070, across the globe) (see Methods). For the ENM approach, we classified present-day predation pressure into low (corresponding to the lower 50% of the current distribution of predation pressure) or high predator attack rates (spanning the upper 50% of the distribution), respectively (Fig. 2). Then, we performed ENM to predict the distribution of each of these classes under current and future climate scenarios, using the four key temperature variables identified by our structural equation model (Fig. 1b and Supplementary Fig. 1) and an ensemble of two general circulation models (GCMs)—the Model for Interdisciplinary Research on Climate 5 (MIROC5) and Community Climate System Model 4 (CCSM4)—and two representative concentration pathways of CO_2 emission (RCPs)—RCP4.5 and RCP8.5 (see Methods for details). The same GCMs, RCPs and temperature variables as used in ENM were used to build individual predictive GLMM maps.

According to the ENM, the current prevalence of high predation pressure increased towards lower latitudes (Fig. 2a), whereas low predation pressure dominated at higher latitudes (Fig. 2b). These patterns were similar for both RCPs used (Fig. 2 and Supplementary Figs. 3–5). However, the latitudinal gradient was not uniform. Some temperate and polar regions (notably, coastal areas in southern Oceania, Patagonia and northern Europe) were predicted to be characterized by strong predation pressure, which was otherwise more characteristic of subtropical latitudes (Fig. 2).

Extending the ENM of predation pressure to future climate scenarios revealed a decline in the area experiencing high predation pressure at lower latitudes, and an increase of suitability for high predation pressure at higher latitudes (Fig. 2, Supplementary Figs. 3–5 and Supplementary Table 2). Indeed, modelling the difference of future (2050 and 2070) and current climate scenarios (that is, projected difference over time) revealed qualitatively similar results at the site (GLMM) and projected global levels (ENM). Both approaches suggested decreasing predation pressure towards lower latitudes, and a remarkable increase of predation pressure towards higher latitudes (Figs. 3 and 4). These patterns were similar for both GCMs used, and were not affected by whether we used sites or plots (within sites) as our data points (see Supplementary Fig. 6 and Supplementary Table 3). However, the GLMM predictions also revealed a projected decrease of predation pressure at northern latitudes (consistent across Alaska and Greenland; Fig. 3 and Supplementary Figs. 7–9), which—if borne out—will come with a major effect on the local ecosystems, yet was not detected by ENM. These inconsistencies in the details between the two modelling approaches are probably due to the high uncertainty of ENM projections (Supplementary Table 2), especially at the extremes of the current data range. Since projected climate predicts stronger changes in the range and instability of temperature than in average temperatures (Supplementary Fig. 10), and since these changes are predicted to be stronger in the tropics than in temperate zones (Supplementary Fig. 11), the observed decline in tropical predation pressure is probably due to the climatic instability predicted for this region in the near future (Supplementary Figs. 10 and 11). This decline in predation pressure was pronounced inland, but not in coastal areas, where ocean temperature may buffer climatic instability in the future.

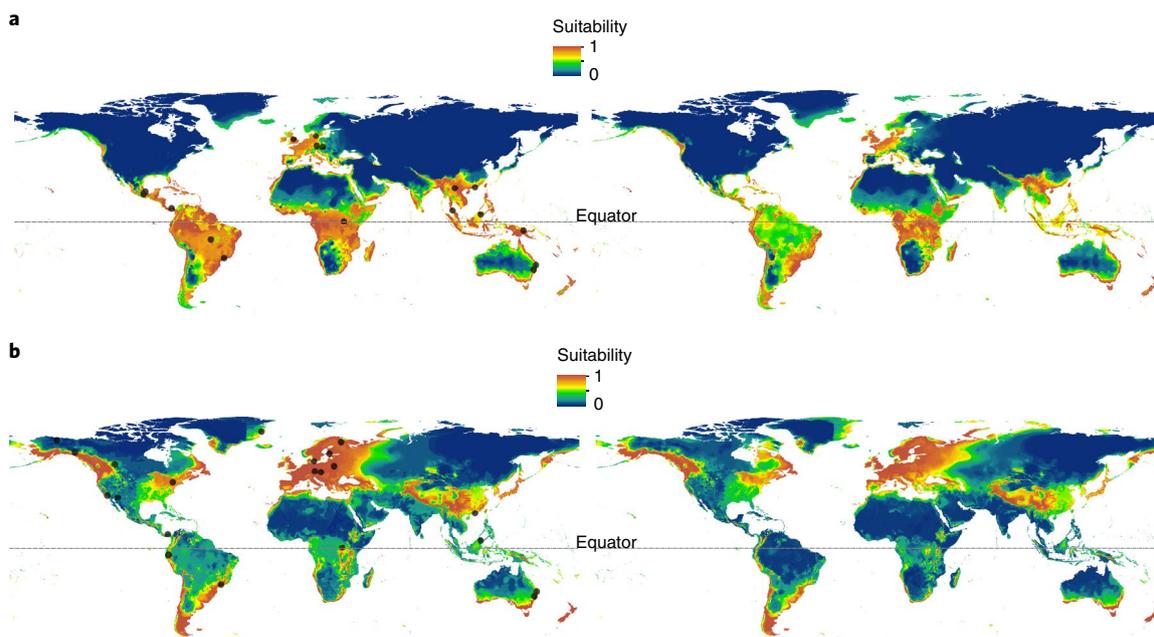


Fig. 2 | Global distribution of high and low predation pressure under the current climate (2015) and a climate scenario projected for 2070. a, b, We classified the predation pressure into two classes: high (**a**; $n = 62$ occurrence points) and low (**b**; $n = 92$). Current (left) and projected (right) distributions of predation pressure are shown for each class (see Methods for details). The niche model was based on the four major temperature components identified by the PCA (Supplementary Fig. 1), assuming an ensemble of CCSM4 and MIROC5 GCMs (RCP4.5) (see Methods for details). Black dots show the sites according to each category of predation pressure.

Overall, multiple components of climate—especially temperature—explained latitudinal and elevation patterns of predation better than latitude or elevation by themselves. Our results also show that future changes in climatic conditions could rearrange the global distribution patterns of biotic interactions—adding a new dimension to climate change impacts. Recent advances in climatic models and spatial modelling tools, in combination with availability of the detailed global databases, allow us to predict that arthropod predation pressure would increase with warming but decrease with climatic instability, especially at lower latitudes. As a particular asset, access to replicated experimental data obtained by a standardized protocol, acquired and analysed in a consistent way¹⁴, improved the signal-to-noise ratio in our findings.

The dependence of arthropod attack rates on temperature variables is strongly supported by our understanding of organismal physiology. The pattern is driven by arthropods¹⁴, which—as ectotherms—are closely dependent on external energy. Warming enhances arthropod metabolic activity, food consumption rates^{22,23} and reproductive rates²³, all of which can increase the magnitude and frequency of trophic interactions^{22,24}. However, temperature increases above the thermal optima of ectotherm predators can destabilize predator–prey dynamics and cause local extinctions²⁴. Moreover, changes in the variance of temperature can have disproportionately greater impacts on individual taxa and whole communities than changes to the mean temperature²⁵. Such variability will be important when it occurs both between different parts of the day and between different parts of the year, as both types of variation will constrain the activity period of ectotherms, and as temperature extremes will affect the mortality rates experienced by the predator population itself.

Where previous climate change research has focused on the shifts in species distribution, we have applied conceptually equivalent techniques to model the global distribution of biotic interactions. The application of niche modelling and generalized linear mixed-effects modelling allowed us to identify the areas where predation

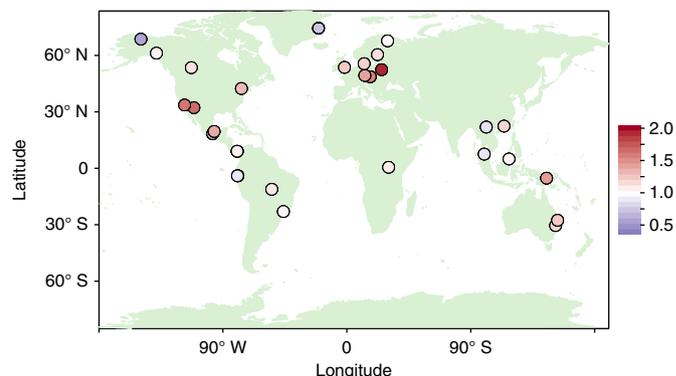


Fig. 3 | Changes in predation pressure predicted by the GLMM approach.

Difference in odds ratios between the future (2070) and current (2015) predation rates. A value of 1.0 implies no change, whereas a value of 2.0 shows a doubling of the odds of an individual caterpillar being attacked per day. Predicted values were obtained from GLMM, based on the four major temperature components identified by PCA (Supplementary Fig. 1), assuming the MIROC5 (RCP4.5) global climate model (see Methods for details).

intensity is expected to increase or decrease in the future. Our model projections of reduced arthropod predation pressure may indicate yield reduction and increased threats to food security, due to a decrease in the efficiency of biological control in the areas that are already most vulnerable under climate change²⁶. In pointing out these concerns, we believe that we serve as important whistle blowers. Yet, we should clearly stress caveats and limits to predictability. At present, we lack information regarding the rate with which biotic interaction strength may adjust to a changing climate. In terms of species distribution change, terrestrial taxa tend to move poleward by an average rate of 17 km per decade²⁷. Differences in species responses can result in novel biotic communities, and altered biotic

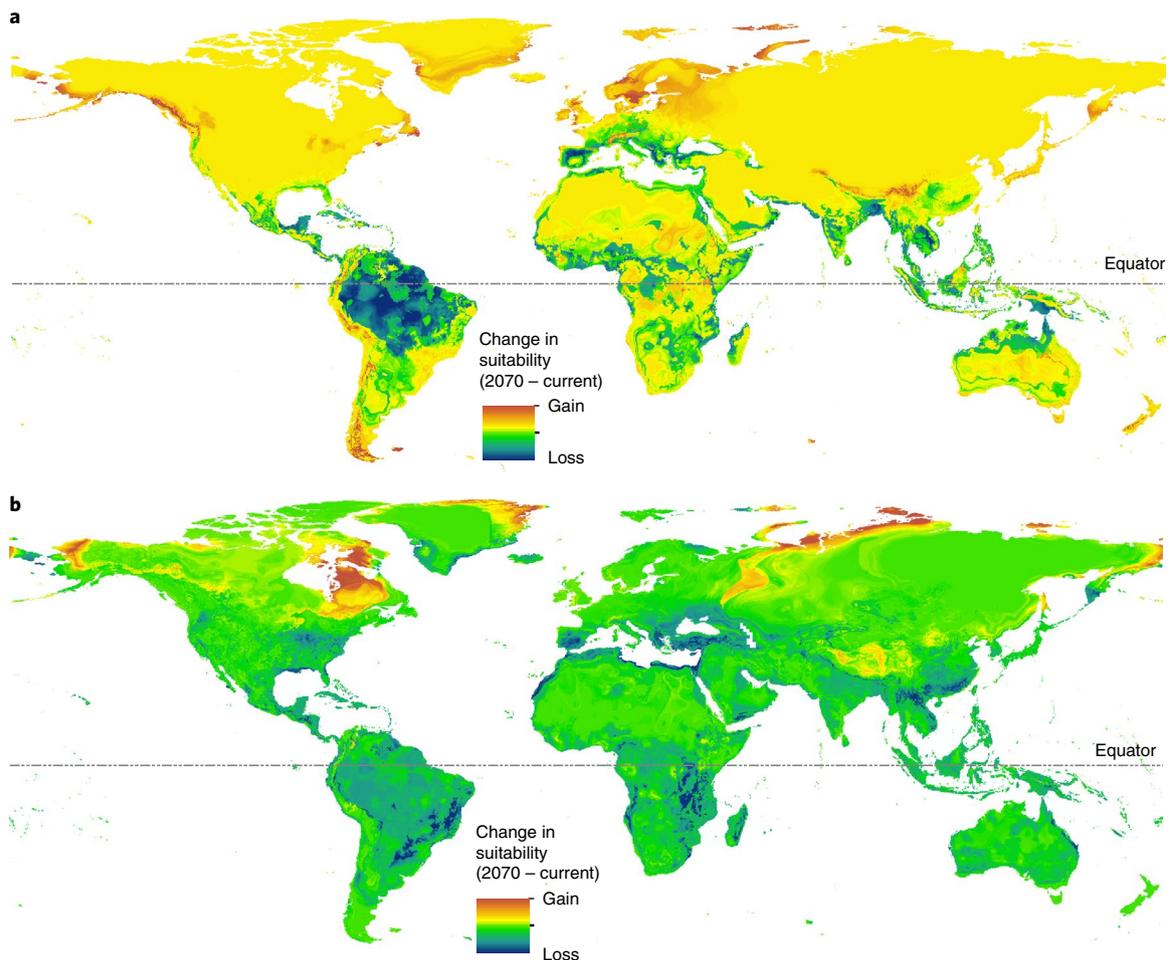


Fig. 4 | Global shift in the suitability of high and low predation pressure between the present-day climate and that of 2070. a,b, Differences between the projected (2070) and current climate scenarios for high (a) and low (b) predation pressure. Blue regions demonstrate that suitability (that is, the likelihood of occurrence of a certain category of predation strength) under the current climate is greater than in 2070, suggesting future loss of suitability, especially at lower latitudes. Sites in brown are predicted to increase (gain) in future suitability. Niche modelling was based on the four major temperature components identified by PCA (Supplementary Fig. 1), assuming an ensemble of CCSM4 and MIROC5 GCMs (RCP4.5).

interactions can either hinder or facilitate further range shifts, often with cascading effects²⁸. A satisfactory understanding of how communities come together and function in a changing climate will call for more than modelling each species on its own or biotic interaction strength separate from community composition and functioning²⁹. Yet, while our current predictions come with major uncertainties, they identify a new avenue for important exploration³⁰.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41558-018-0347-y>.

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Author contributions

G.Q.R. conceived the idea, developed it with all co-authors, and drafted the manuscript with inputs from all co-authors. G.Q.R., T.G.-S. and N.A.C.M. performed the statistical analyses. T.S.-S. performed the niche modelling with inputs from T.G.-S. and G.Q.R. T.G.-S. and T.S.-S. drafted the figures. All authors contributed substantially to revisions and the final format of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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Methods

Experimental design and data. Estimates of local attack rates were derived from a globally distributed experiment of predator attacks on model prey (data from ref. ¹⁴). Briefly, model prey were moulded from green plasticine, shaped and sized as common geometrid caterpillars. A total of 20 prey models were deployed within each of 5 plots at each of 31 sites along a latitudinal gradient spanning from 30.4° S to 74.3° N and an elevation gradient spanning from 0 to 2,100 m above sea level. Together, we monitored the fates of 2,879 model caterpillars over 4 to 18 days, resulting in a total of 12,694 caterpillar days. Whenever an attack was scored, the focal caterpillar was removed without replacement. To avoid observer bias, all participants returned the caterpillars for double-blind scoring by an experienced team at the University of Helsinki. Based on tooth, beak, mandibular or radular marks, all feeding damage on caterpillars was attributed to one of six predator groups: birds, lizards, mammals, arthropods, gastropods or an unknown predator. Intact caterpillars were scored as being not attacked, whereas the few caterpillars not retrieved were excluded from all analyses. Arthropods accounted for the vast majority of attacks, with clear, latitudinal patterns in attack rates¹⁴. Thus, we focused our analyses on attack rates by arthropod predators per caterpillar-day exposed in the field. For full details, see refs ^{14,31}.

Climatic and topographic variables. To describe local climatic conditions, we extracted local climatic descriptors from WorldClim version 2 (ref. ³²) and ENVIREM³³. For each of 31 experimental sites, we selected 11 climatic variables, water deficit and topography, which are available at a spatial resolution of 30 arcsec (~1 km at the Equator). The terrain roughness index (TRI; see below) of 3 sites was extracted at a resolution of 2.5 arcmin (~5 km at the Equator) since there were no data available at 30 arcsec for these localities.

The climatic variables were extracted from WorldClim 2.0 (ref. ³²) datasets (<http://www.worldclim.org/>). The climatic components were: bio1 = annual mean temperature; bio2 = mean diurnal range (mean of monthly (maximum temperature – minimum temperature)); bio4 = temperature seasonality (s.d. × 100); bio7 = temperature annual range (maximum temperature of warmest month – minimum temperature of coldest month); bio12 = annual mean precipitation; bio13 = precipitation of wettest month; bio14 = precipitation of driest month; and bio15 = precipitation seasonality (coefficient of variation). The variable associated with water deficit, obtained from the ENVIREM dataset³³, included the Thornthwaite aridity index (hereafter 'aridity'), which measures the degree of water deficit below water need³². This index expresses the relative aridity of a month, comparing differences between precipitation and potential evapotranspiration, where values near 0 represent arid environments. Sites defined as being climatically more unstable were those characterized by higher intra-annual (for example, bio4 and bio7) or diurnal (for example, bio2) variations³⁴.

The topographic variables, which reflect elevation variability in a certain area or pixel, were TRI and topographic wetness, both of which were extracted from the ENVIREM database³³. TRI denotes the local variation in seabed terrain compared with a central pixel. This index approaches 1 in flat terrains, and increases positively with terrain roughness³⁵. Topographic wetness denotes elevation above channel networks, reflecting lateral water accumulation and the moisture status of a particular area³⁶.

Statistical analyses. Causal relationships. To explicitly test the influence of latitude, elevation and their interaction on components of climate, and how components of climate and topography (TRI and topographic wetness) influence arthropod predation pressure (the fraction of caterpillars attacked by arthropod predators per day), we fitted a causal model through structural equation modelling using the piecewiseSEM package³⁷. SEM is a suitable tool for evaluating direct and indirect effects in ecological systems³⁸. The piecewise models were built by GLMM (using the function `glmer` with binomial family) or using linear mixed-effects models (with the function `lme`). Since the original predation experiment¹⁴ deployed 20 model caterpillars within each of 5 plots at each of 31 sites, we used plot nested within site as a random effect in both generalized linear mixed-effects models and linear mixed-effects models. To construct these models, which directly tested the effect of temperature and precipitation on predation pressure, we first performed separate PCAs for the climatic components of temperature (bio1, bio2, bio4 and bio7) and precipitation (bio12, bio13, bio14, bio15 and aridity). We then used the first orthogonal axis (PC1) of temperature (explaining 71.2% of the variation) and precipitation (explaining 53.0% of the variation) as endogenous predictors of predation pressure in the SEMs. We performed these two PCAs using the functions `rda` (vegan package) and `prcomp` (stats package). The predictors PC1_{temperature} and PC1_{precipitation}. TRI and topographic wetness were not collinear (variance inflation factor < 2.07). Model fits were evaluated using Shipley's test of d-separation through Fisher's C statistic³⁷.

Current and projected climate variations. The range of variation for each bioclimatic descriptor of temperature (bio1, bio2, bio4 and bio7) was calculated as the difference between the projected and current climate. Before calculating the range of all bioclimatic variables, we standardized their values between 0 and 1 to prevent spurious comparisons between variables on different scales. Then, we subtracted the projected (future) values from the present values of each bioclimatic variable.

Short arrows (for example, bio1 in Supplementary Fig. 10) indicate small changes in temperature features in the near future (2050 and 2070) and long arrows (bio2, bio4 and bio7) indicate big changes in temperature in the near future. These calculations were done for two independent GCMs (MIROC5 and CCSM4).

We also used an orthogonal Procrustes analysis to estimate the variation between current and projected future climate for temperate and tropical regions. We selected only the significant variables used in the SEM model (that is, bio1, bio2, bio4 and bio7). Here, we first performed a PCA on both current and projected climate, previously standardized to vary between 0 and 1. We then applied the Procrustes analysis to superimpose the two datasets (PCA scores) while minimizing (by rotation and mirror reflection) the sum of squared distances between them. We did not intend to calculate the concordance between the two matrices (that is, the m^2 statistics³⁹). Instead, we produced the typical Procrustean plot (Supplementary Fig. 11) and calculated the Euclidean distance (that is, the length of the arrow) between the reference matrix (PCA_{current}) and rotated PCA scores of the projected climatic variables (PCA_{projected}). Because PCA scores represent the linear combination of raw (standardized) data, the position (score) of each site in the two-dimensional space indicates its 'mean' climate value. Therefore, the further the position of the reference (current climate) from the rotated (future climate) score, the higher the variation of bioclimatic variables. In addition, loadings can be used to estimate the contribution of bio1, bio2, bio4 and bio7 to the climatic variation between present and future projections. Therefore, the length of the arrow in the Procrustean plot indicates the variation between the current and future climate; sites with longer arrows are expected to experience greater climate change.

All the statistical analyses were performed using the language environment R⁴⁰. The significance level chosen was $\alpha = 0.05$. We checked variance heterogeneity, normality and outliers through graphical evaluation (for example, Q-Q plots, Cook's distance and influence). We also tested and corrected for overdispersion in the models with binomial family (GLMM).

Predicting predation pressure. To map the effect of future climate change on the global distribution of predation pressure, we applied two complementary approaches: (1) ENM and (2) GLMM.

ENM. ENM approaches are used to predict species distribution patterns over time^{41,42}. Basically, ecological niche models use the relationship between known occurrence points and environmental variables (mainly climate⁴³) to predict suitability values at unknown sites.

Here, we used empirically estimated predation pressure as occurrence points from a global dataset of arthropod predator attacks on plasticine caterpillar models¹⁴. Since ENM deals with presence-only modelling^{41–43}, and the attack rate is a proportion bound between 0 and 1 (ref. ¹⁴), we first transformed continuous probabilities to categorical variables. Predation pressure within each experimental plot was discretized into two classes (0–50% and >50–100%), scoring a presence when local attack rates fell within the respective class limits: low (0–50%) and high (>50–100%). The transformation of continuous variables to categorical is common practice in analyses of macroecological patterns⁴⁴, and the results remained qualitatively unchanged whether we categorized attack rates into two (present analysis) or three classes (0–25, 26–75 and 75–100%; results not shown). After identifying the temperature components of climate as the main drivers of predation pressure using SEMs, we used the mean annual temperature, mean diurnal range, temperature seasonality and temperature annual range (bio1, bio2, bio4 and bio7) as variables for the ecological niche models. We modelled the current climate scenario, and those projected to 2050 and 2070, using an ensemble of MIROC5 and CCSM4 GCMs (RCP4.5 and RCP8.5).

To predict the spatial distribution of each class of predator attack rates, we used an ensemble forecasting approach^{45,46}. For this, we built ecological niche models using four algorithms: (1) Envelope Score (Bioclim)⁴⁷; (2) Domain (Gower Distance)^{48,49}; (3) Maximum Entropy⁵⁰; and (4) Support Vector Machines⁵¹. We shared the occurrence points in two subsets: 75% for training models and 25% to test (evaluate) models. As training and test points are part of the same occurrence dataset, we randomized this step ten times to minimize bias in the spatial structure. We inferred a maximum sensitivity and specificity threshold (as proposed by ref. ⁵², by using a presence-only method) and calculated the true skilled statistic (TSS)⁵³ and AUC values to evaluate each model. Values of TSS vary from –1 to +1. Models presenting values of TSS higher than 0 differ from random models, and values higher than 0.5 are assumed to be adequate⁵³. We also evaluated the models using the area under the curve (AUC) of the receiver operator characteristic; values of AUC vary from 0 to 1. Models with AUC values higher than 0.5 differ from random models, and those higher than 0.7 are considered adequate⁵⁴. Uncertainty was evaluated using s.d.⁵⁵. TSS, AUC and s.d. values for each algorithm above are presented in Supplementary Table 2. To predict the worldwide suitability of each category of predation pressure (low and high) under each climate scenario, we overlapped the models using different algorithms based on the weighted average by TSS value. The suitability values (that is, likelihood of occurrence) ranged from 0 (low suitability) to 1 (high suitability).

GLMM. To validate the results of our niche modelling approach by a separate technique, we modelled predation pressure as a continuous response using GLMM.

Arthropod attack rates observed at each site were fitted to a generalized linear mixed-effects model with plot nested within site as a random effect. As independent, continuous variables, we included the four bioclimatic variables of temperature (bio1, bio2, bio4 and bio7) retained in our structural equation model (note that we opted to use separate climatic variables rather than the principal components identified in the structural equations above, since the structure of correlations among variables may shift with climate change). Since the response was a probability (attack rate per capita per day), we assumed a logit link and binomially distributed errors. We then used the function `predict.merMod` in the package `lme4` in R to generate predicted values for the response variable (attack rate) under current and future climate (2050 and 2070). Climatic conditions under future scenarios were extracted from two different GCMs—MIROC5 and CCSM4 (RCP4.5 and RCP8.5). Finally, as a clear-cut metric of expected change, we derived and mapped site-specific odds ratios of predation risk under current versus future (2050 and 2070) climatic conditions (Fig. 3 and Supplementary Figs 7–9).

Data availability

The data that support the findings of this study are publicly available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.j432q>.

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