

LATITUDINAL GRADIENTS

Higher predation risk for insect prey at low latitudes and elevations

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Biotic interactions underlie ecosystem structure and function, but predicting interaction outcomes is difficult. We tested the hypothesis that biotic interaction strength increases toward the equator, using a global experiment with model caterpillars to measure predation risk. Across an 11,660-kilometer latitudinal gradient spanning six continents, we found increasing predation toward the equator, with a parallel pattern of increasing predation toward lower elevations. Patterns across both latitude and elevation were driven by arthropod predators, with no systematic trend in attack rates by birds or mammals. These matching gradients at global and regional scales suggest consistent drivers of biotic interaction strength, a finding that needs to be integrated into general theories of herbivory, community organization, and life-history evolution.

It is widely accepted that species diversity increases toward the tropics (1). This gradient is so ubiquitous that it has been called one of the fundamental laws in ecology (2). However, whether this latitudinal variation in diversity is paralleled by similar gradients in the intensity of biotic interactions, both antagonistic and mutualistic (3–9), remains unclear.

A widespread view is that biotic interactions become increasingly strong at lower latitudes (10–12). However, accumulating evidence [e.g., (7, 8, 13, 14)] suggests that when critically examined, this pattern may be weak, absent, or even reversed. Part of this complexity arises because large-scale patterns are usually pieced together from data obtained by a variety of methods and protocols [e.g., (7, 15, 16)]. Here we use a simple, uniform protocol to quantify ecologically impor-

tant patterns systematically at a global scale (17, 18). Specifically, we assess predation risk using the attack rate on model caterpillars (Fig. 1) for which the identity of the attacker may be determined (19). This method has been shown to provide accurate estimates of predator activity at individual sites and across local gradients (20, 21). By applying a consistent method at a global level, our study provides a rigorously controlled estimate of latitudinal patterns in predation strength.

Building on general theory (3, 10, 11), we hypothesize that overall biotic interaction strength increases toward the equator. Many ecological factors that change with latitude also change with elevation, and thus it is important to control for elevational variation when quantifying latitudinal signals in predation rates. Moreover, by testing for congruence between latitudinal and elevational

predation patterns, we can begin to identify candidate mechanisms underlying predation rates.

Regardless of where high predation rates are found, depredation of herbivores is predicted to have broad ecological and evolutionary consequences across trophic levels. Stronger predation on herbivores directly affects the abundance and traits of herbivores (22–24), but also indirectly affects the abundance and traits of plants through trophic cascades (25, 26). Gradients in interaction strength thus provide a foundation for understanding global patterns in ecosystem processes (e.g., herbivory and primary production), ecosystem services (e.g., carbon storage and crop yields), and how long-term environmental change may affect biodiversity.

Predation rates reflect the sum of attacks by several different predator groups, each of which may show a different latitudinal pattern. We expect predation by ectothermic predators such as arthropods to be strongly controlled by local abiotic conditions. Indeed, temperature has been identified as the dominant abiotic factor directly affecting ectothermic insects (27, 28), and in experiments, insect performance generally improves with temperature (29). An increase in the intensity of insect-mediated biotic interactions with increasing mean temperature is also supported by the higher folivory rates observed during warmer geological periods (30, 31). Thus, we expect increased attack rates by arthropod predators at low latitude and low elevation. By contrast, endotherms such as insectivorous birds may redistribute themselves through migration in response to local food availability (32). This is expected to homogenize predation rates across latitude and elevation or elevate predation rates in their higher-latitude breeding grounds.

To test these hypotheses, we systematically measured predation risk by monitoring the fates of 2879 model caterpillars over 4 to 18 days, resulting in a total of 12,694 caterpillar days (table S1). These caterpillars were molded from green plasticine, shaped in the posture of common generalist caterpillars, and deployed within five 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 2100 meters

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above sea level (masl). Whenever an attack was scored, the caterpillar in question was removed without replacement. We used generalized linear mixed-effects models (33) to quantify the effects of latitude and elevation on biotic interaction strength, measured as the probability of a caterpillar being attacked per day exposed [for further validation of this response, see (33)].

Consistent with our predictions, we found that predation rates were highest at the equator and decreased significantly toward the poles (Fig. 1A; $F_{1,27.8} = 10.28$, $P = 0.003$). For every 1° of latitude away from the equator, the daily odds of a caterpillar being attacked decreased by 2.7% (odds ratio

0.973, confidence limits 0.959 to 0.987; Fig. 1A). Thus, at the highest latitude studied (74.3°N; Zackenberg, Greenland), the daily odds of a caterpillar being attacked by a predator were only 13% (odds ratio 0.131, confidence limits 0.046 to 0.376) of the odds at the equator. Predation rates also decreased with increasing elevation ($F_{1,27.1} = 6.35$, $P = 0.02$; Fig. 1D), independent of latitude (i.e., no latitude by elevation interaction; $F_{1,27.8} = 0.70$, $P = 0.41$). For every 100 m moved upward from sea level, the daily odds of predation decreased by 6.6% (odds ratio 0.934, confidence limits 0.884 to 0.987). At the highest elevation studied (2106 masl, table S1), the daily odds of predation were 24% of those

at sea level (odds ratio 0.238, confidence limits 0.074 to 0.765).

Notably, higher predation at lower latitudes and elevations was due to more frequent attacks by arthropod predators. The daily odds of a caterpillar suffering an arthropod attack decreased by 3.5% for every 1° latitude moved away from the equator (odds ratio 0.966, confidence limits 0.947 to 0.984, $F_{1,25.1} = 14.11$, $P < 0.001$), as did the odds of attack marks that could not be attributed to any specific predator group (odds ratio 0.972, confidence limits 0.954 to 0.991, $F_{1,24.3} = 9.57$, $P = 0.005$; Fig. 1C). By contrast, we found no evidence for a gradient in predation by birds or mammals;

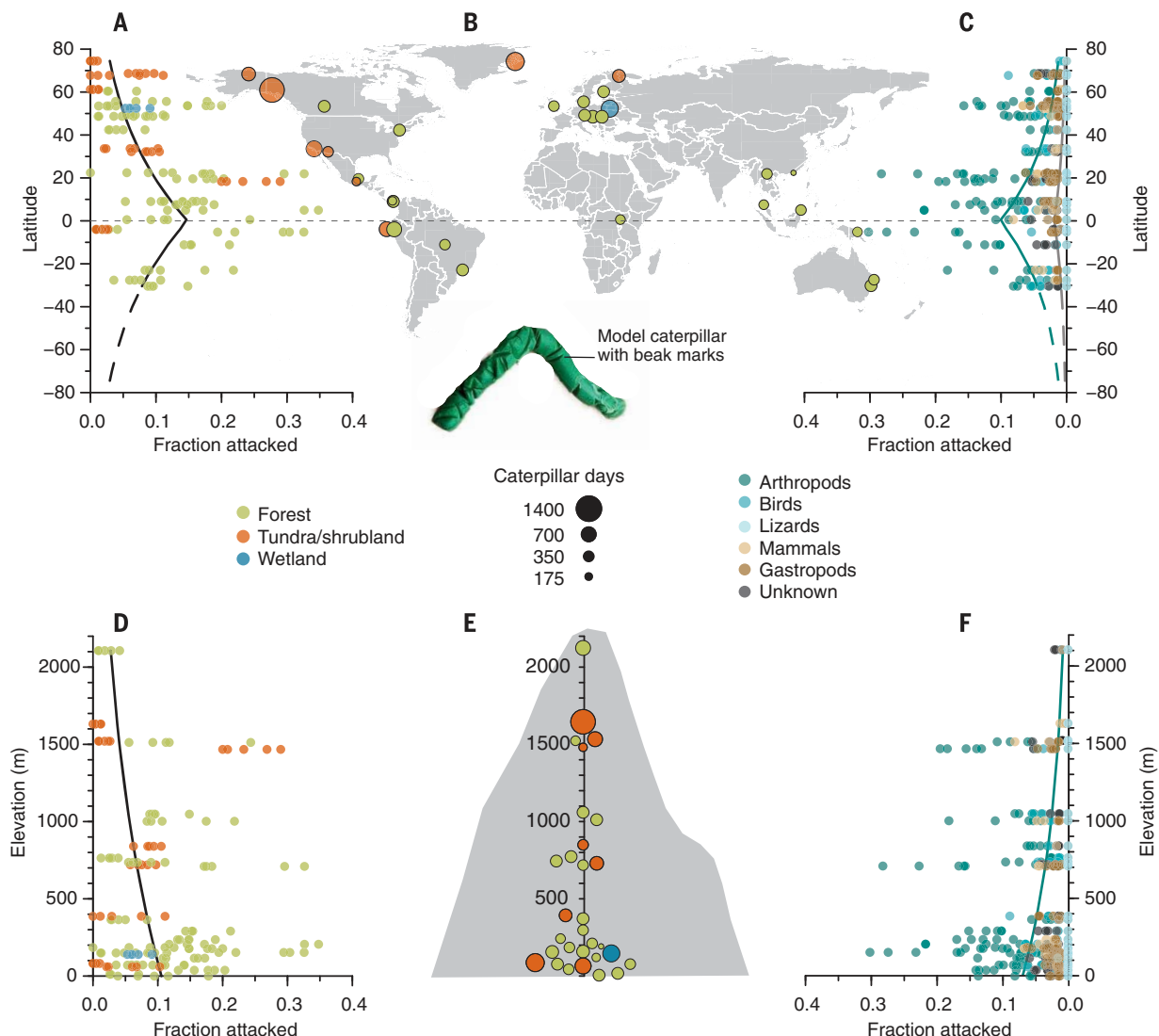


Fig. 1. Map of sampling sites with scatter plots showing fates of model caterpillars at different latitudes and elevations. (A to F) In the map of sampling sites across the globe (B) and across elevations (E), individual sites are shown with symbol size graduated by caterpillar days and habitat type identified by the symbol color. For site-specific details, see table S1. (A) and (D) show the overall fraction of caterpillar models attacked per day (i.e., daily predation rates per model caterpillar) in each habitat type, with the patterns resolved by predator type in (C) and (F). Each individual data point reflects the fate of replicate model caterpillars in one of five sampling plots within a

site (horizontal line of data points) (33). Data points are partially transparent and appear darker when overlapping. Curves show values fitted by logistic generalized linear mixed-effects models (33), including only responses for which a significant association with latitude was found [with the green curve in (C) and (F) corresponding to arthropod attack and the gray curve in (C) to unclassifiable attacks]. Dotted lines in (A) and (C) represent extrapolation beyond the data range, included to demonstrate symmetry around the equator. (B) also shows a model caterpillar deployed in Northern Finland, showing extensive beak marks typical of a bird attack.

the frequencies of attack marks by these predator groups were unrelated to latitude ($F_{1,26.6} = 1.20$, $P = 0.28$ and $F_{1,28.6} = 2.9$, $P = 0.10$, respectively). These latitudinal patterns in predation rate were mirrored across elevation: The odds of a caterpillar suffering arthropod attack decreased by 9.6% for every 100 m moved upward from sea level (odds ratio 0.904, confidence limits 0.839 to 0.975, $F_{1,26.1} = 7.48$, $P = 0.01$), whereas the odds of receiving attack marks not attributable to any specific predator group ($F_{1,21.3} = 0.18$, $P = 0.68$) or of being attacked by birds ($F_{1,29.3} = 1.86$, $P = 0.18$) or mammals ($F_{1,25.0} = 0.63$, $P = 0.44$) were unrelated to elevation (Fig. 1F).

Overall, our study reveals a strong latitudinal and elevational signature on biotic interaction strength (i.e., predation rates) across the globe. In doing so, it provides a clear pattern that can be used to inform future efforts in this field (3–7) and to move beyond the obstacle of contradictory evidence from variable methodologies among studies conducted at different subsets of latitude (7, 13). The parallel patterns in predation across elevation [compare (27)] suggest that the ecological factors constraining predation rates are likely to show concordant latitudinal and elevational gradients (34). The clarity of our findings offers a simple lesson: To unmask a global ecological pattern, we may need to apply standardized methods to specific hypotheses determined a priori, rather than combine data derived from different methods a posteriori [compare (8, 13, 34)]. This study thus illustrates the power of simple, low-cost, globally distributed experiments [compare (17, 18, 35)].

We found that global gradients in predation rate were driven by arthropod predators, with no systematic trend in attack rate by birds or mammals. This latitudinal shift in the relative importance of different predator groups has clear implications for understanding herbivore evolution, interpreting global patterns of herbivory, and understanding global community organization and functioning. In terms of arthropod herbivore evolution, much theory has been developed on latitudinal patterns in plant defense against herbivores, suggesting that if plants at lower latitudes suffer high herbivory, they need to evolve stronger defenses [e.g., (10, 11, 15)]. Our findings motivate an analogous theory for defense deployed by herbivores against their predators. In the tropics, the fraction of model caterpillars attacked per day is notably high (Fig. 1), and attack rates on live prey tend to be even higher (35). Thus, predation in the real world creates a very real selection pressure. This leads to the testable hypothesis that arthropod herbivores in the

tropics should be better defended than those at higher latitudes and that these defenses should target arthropod rather than vertebrate predators (Fig. 1C).

Real herbivores accumulate predation risk over their development time, which may be shortened in warmer climates and thus counteract our predictions for the ecological and evolutionary impact of predation gradients. Although a comprehensive assessment goes beyond the current study, we analyzed larval development times from the available literature (table S2), finding a much lower latitudinal effect on development times than on predation rates (table S3). Hence, as a net effect, we expect increased selection pressure on larval herbivores at lower latitudes.

From a plant perspective, the patterns detected in this study suggest increased per capita predation pressure on plant consumers toward the tropics and strong differences in the relative impacts of different predator groups across different regions of the globe (Fig. 1C). This finding suggests markedly different roles for different predator groups in regulating herbivore abundance and traits across geographic gradients, and potential differences in trophic organization between regions. Whether the patterns revealed by the current study translate into patterns in net herbivory is unresolved, particularly considering that our experiments took place in the understory, whereas most primary production takes place in the canopy layer. Although seminal findings suggested latitudinal gradients in herbivory and plant defense (15, 16), recent appraisals of the evidence find less support for these trends (7, 8, 14). Nonetheless, the lack of clear patterns in herbivory may be as much a reflection of variable methods as a true lack of a pattern (7, 13, 15, 16, 36). The current study should stimulate further standardized comparisons of species interactions, facilitating a clearer view of these key biological patterns to enlighten our search for their drivers and consequences.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Supplementary Text
Fig. S1
Tables S1 to S3
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Editor's Summary

Risky in the tropics

It is well known that diversity increases toward the tropics. Whether this increase translates into differences in interaction rates among species, however, remains unclear. To simplify the problem, Roslin *et al.* tested for predation rates by using a single approach involving model caterpillars across six continents. Predator attack rates were higher toward the equator, but only for arthropod predators.

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