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Global change biology

Changes in the background losses of woody plant foliage to insects during the past 60 years: are the predictions fulfilled?

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The existing scenarios generally predict that herbivory will increase with climate warming. An analysis of the published data on the background foliar losses of woody plants to insects in natural ecosystems across the globe from 1952 to 2013 provided no support for this hypothesis. We detected no temporal trend in herbivory within the temperate climate zone and a significant decrease in herbivory in the tropics. From 1964 to 1990, herbivory in the tropics was 39% higher than in the temperate region, but these differences disappeared by the beginning of the 2000s. Thus, environmental changes have already disturbed one of the global ecological patterns—the decrease in herbivory with latitude—by affecting ecosystem processes differently in tropical and temperate climate zones.

1. Introduction

Insect herbivory affects the productivity of ecosystems, modifies nutrient cycling, maintains the diversity of plant communities and influences a number of ecosystem services [1,2]. Consequently, the relationships between plants and insects are among the most intensively studied biotic interactions [3,4], and the exploration of changes in insect–plant relationships caused by the abiotic drivers of global change has become increasingly popular during the past decades. The existing scenarios generally predict that increasing temperature will cause faster increases in herbivory than in plant productivity [5–7], although the suggested mechanisms behind this prediction are diverse. Population densities of plant-feeding insects were predicted to increase because of direct beneficial effects of warmer climate on insect herbivores [8] and adverse effects of increased climatic variability on their natural enemies [9]. Furthermore, consumption of foliage was expected to intensify because of the nitrogen dilution effect associated with an increase in CO_2 concentrations [10] and increased metabolic demands of insects under higher temperatures [11]. These predictions are supported by the positive association noted between herbivory and mean temperature of the growth season observed along latitudinal gradients outside the tropics [12], as well as by palaeontological data that show enhanced herbivory with climatic warming in the past [13]. As far as we know, none of the existing scenarios has considered a decline in herbivory with climate warming or the maintenance of the pre-industrial level of herbivory, although many researchers [11,14,15] have appreciated the high variability in the relationships between the abiotic drivers of global changes and herbivory and, consequently, the uncertainty in predicting community-wide changes in plant foliar losses to insects.

The recent mean global temperature is about 0.8°C higher than it was in 1880–1920. Two-thirds of this temperature rise has occurred since 1975, at a rate of roughly 0.15–0.20°C per decade [16], and the trends in temperature changes were generally consistent between tropical and non-tropical regions

during the period covered by our data (National Oceanic and Atmospheric Administration (NOAA) data on temperature anomalies: $r = 0.80$, $n = 65$ years, $p < 0.0001$). This warming has been associated with a wide range of biological changes. The empirical evidence on the effects of climate warming on insects concerns, in particular, changes in phenology and distribution [17] and increasing plant damage by some pest species [15]. To our knowledge, no attempts have been made to check whether the losses of plant foliage to insects have increased during the past decades at the global scale. In this study, we tested the hypotheses that herbivory on woody plants has increased during the past 60 years, and that this increase has been similar across climatic zones.

2. Material and methods

We searched the data on the total background losses of woody plant foliage to insects (quantified as the percentage of leaf area or biomass consumed or otherwise damaged by defoliating, mining and galling species, whose populations were at their 'normal' densities, at a certain locality in a certain year) in natural ecosystems. The databases, keywords and criteria used in the selection of papers and the details of data extraction are provided in the electronic supplementary material, appendix S1.

The percentage of the leaf area lost to insects was log-transformed to meet the normality assumption and averaged separately by the year of data collection within the tropical and temperate climate zones (the amount of data from the polar region was insufficient for the analysis). To minimize the impacts of variation among individual estimates of herbivory on the resulting pattern, we excluded the low accuracy means that were based on only one to four estimates of foliar losses. The relationships between the year of data collection and herbivory in the tropical and temperate climate zones were compared by ANCOVA and then quantified by calculating Pearson correlation coefficients within each climate zone [18].

3. Results

We identified 193 papers (published from 1961 to 2015) that fit our search criteria (electronic supplementary material, appendix S1). These papers reported 1569 values of the percentage of leaf area consumed or damaged by insects, which were measured during 1952–2013 from at least 643 species of woody plants (some plants were not identified to the species level) belonging to 116 families (electronic supplementary material, appendix S2). The data originated from 479 localities across the globe and are based on investigations of over 1 370 000 leaves.

The foliar losses of woody plants to insects showed different relationships with study year in tropical and temperate climate zones (ANCOVA, interaction between the zone and the year: $F_{1,61} = 14.6$, $p = 0.0003$). Herbivory significantly decreased with the year of data collection (figure 1 and electronic supplementary material, appendix S3) or with increase in temperature anomalies ($r = -0.52$, $n = 27$ years, $p = 0.0002$) in the tropics, but did not change in the temperate zone (figure 1 and $r = 0.01$, $n = 41$ years, $p = 0.77$, respectively). The 95% confidence intervals of the regressions of herbivory on study year in tropical and temperate zones started to overlap in 1990.

4. Discussion

Although causal relationships cannot be inferred from the negative correlation found between the year of data collection and herbivory in the tropics, the long-term temporal trends in characteristics of biota are usually associated with changes in temperature and precipitation during the observation period [19]—assuming that a plausible explanation of the mechanisms behind the detected changes is provided. We attribute the decrease in foliar losses of tropical woody plants to insects to adverse effects of increasing temperature, because both consumption rates and fitness of herbivorous insects (which are ectothermic organisms) decline sharply once a species encounters temperatures beyond its thermal optimum [20]. Insects in the tropics are currently living very close to their optimal temperatures [21]; thus, even relatively minor temperature increases may have detrimental effects. Some evidence suggests that climate warming may adversely affect insect herbivores also in the temperate zone [22].

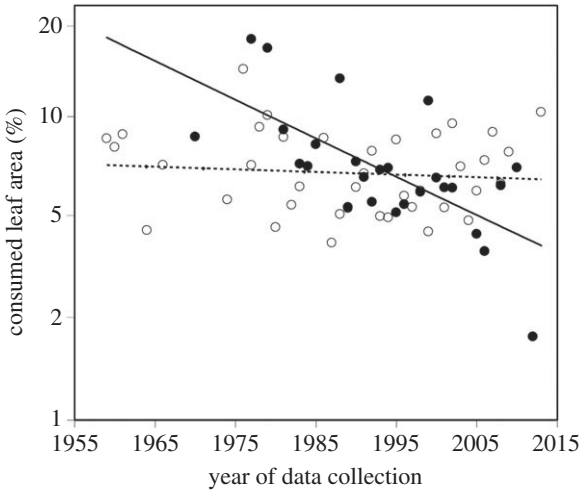

Figure 1. Changes in mean annual foliar losses of woody plants (averaged across study sites and plant species within each climate zone; log scale) to insects in the tropics (filled circles; $r = -0.67$, $p = 0.0002$) and in the temperate climate zone (open circles; $r = -0.09$; $p = 0.57$).

The observed absence of temporal trends in herbivory within the temperate zone can be explained by a broader thermal tolerance of insect species living in this zone when compared with the tropics [21], which would result in their lower sensitivity to climate warming. It may also be a result of the complex and imperfectly understood interactions among environmental and biotic factors, and/or reflect the individualistic responses of herbivore species and their host plants to abiotic drivers of the global climate change [3,4,6,8,14,22].

The temporal trends in biotic data may arise because of changes in research paradigm, which affect the probabilities of collection and publication of a certain type of data [23]. However, the research paradigm regarding the decrease in herbivory from the equator to the poles [24] dominated the research field until very recently [12,25]; therefore, the detected pattern cannot be explained by a paradigm shift. Neither can this pattern be explained by confirmation bias, i.e. the tendency of humans to seek out evidence in a manner that confirms their hypotheses, which was recently found to influence the data on insect herbivory [26]. In the case of confirmation bias, we could detect a strong increase in herbivory with the increase in the year of data collection in both the tropical and temperate climate zones, because several influential publications [5,8] predicted this increase more than a decade ago.

Interestingly, our discovery of the differences in temporal trends in herbivory between the tropical and temperate climate zones sheds new light on the recent discussion of the existence of a latitudinal pattern in losses of plant foliage to insects. In the early 1990s, insect herbivory was suggested to decrease from the equator to the poles [24]. This hypothesis had not been questioned for a long time, but a recent meta-analysis [25] concluded that plant losses to herbivores are independent of latitude. On the other hand, we demonstrated that the losses of woody plant foliage to insects follow a dome-shaped latitudinal pattern: they peak in temperate zones, slightly decrease towards the equator and strongly decrease towards the poles [12]. Our current analysis demonstrated that, by 1990, the herbivory in the tropics was 39% higher than in the temperate region; however, these differences disappeared by the beginning of the 2000s (figure 1). Thus, the past environmental changes have already disturbed one of the global ecological patterns—the decrease in herbivory with latitude—by affecting ecosystem processes in tropical and temperate climate zones in a different fashion.

To conclude, the analysis of the published data provided no support for the hypothesis proposing an increase in the background herbivory with global environmental changes. Instead, we detected no temporal trend in the background foliar losses of woody plants to insects within the temperate climate zone and a significant decrease in these losses in the tropics.

Data accessibility. The data are available from the electronic supplementary material.

Authors' contributions. The authors contributed equally to this study.

Competing interests. The authors declare that they have no conflict of interest.

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