RESEARCH PAPERS

Global patterns in background losses of woody plant foliage to insects

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ABSTRACT

Aim Latitudinal patterns in biotic interactions, particularly in herbivory, have been widely debated. We conducted a quantitative research synthesis to test whether background losses of woody plant foliage to insects generally decrease from the equator to the poles, and whether geographical gradients in insect herbivory are stronger at higher latitudes than at lower latitudes.

Location Global terrestrial ecosystems.

Methods We used published and original data (3482 point estimates of the percentage of leaf area consumed by insects, collected from 941 species of woody plants in 836 localities world-wide) to analyse the geographical patterns in total losses of plant foliage and in losses to defoliating, leaf mining and leaf galling insects separately, and we searched for climatic factors that can explain the variation in the levels of background insect herbivory across the globe and within climate zones.

Result On average, according to published data woody plants lose 7.55% of their leaf area to insects, but 4.73% according to our original data collected in a blinded way. These losses demonstrate a dome-shaped latitudinal pattern: they peak in temperate zones, slightly decrease towards the equator and strongly decrease towards the poles. This pattern is consistent between published and original data, indicating the robustness of the detected relationship between herbivory and latitude. The climatic factors explaining these latitudinal patterns in insect herbivory differ between climate zones.

Main conclusions Our study provides solid support for the hypothesis of a decrease in background herbivory with latitude, but only outside the tropics. For the first time we demonstrate that the latitudinal gradient in insect herbivory across the globe is nonlinear, i.e. its slope differs between the climate zones. In temperate and polar zones, but not in the tropics, background herbivory correlates with mean air temperatures and is therefore likely to increase with climate warming.

Keywords

Background herbivory, climate, defoliators, gallers, geographic pattern, latitudinal variation, miners, research bias.

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INTRODUCTION

Herbivorous insects are ubiquitous in terrestrial ecosystems: it is nearly impossible to discover a mature plant growing in its natural environment that bears no marks of insect feeding. However, until very recently the phenomenon of background, or endemic, herbivory (i.e. damage to plants occurring when herbivore populations are at their 'normal' densities) attracted little attention from scientists, in contrast to severe defoliation resulting from outbreaks of eruptive species.

Losses of plant foliage due to background herbivory are relatively minor, 5–18% of the foliar biomass annually (Cyr & Pace, 1993; Coley & Barone, 1996; Turcotte *et al.*, 2014b). However, several experiments have consistently shown that even relatively minor herbivory may decrease plant fitness (Marquis & Whelan, 1994; Mueller *et al.*, 2005; Zvereva *et al.*, 2012). These findings suggest that variations in background herbivory can shape the evolution of plant defences and demonstrate the need to explore the impacts of low-level chronic herbivory on ecosystem structure and functions (Wolf *et al.*, 2008). This task, in turn, requires

identification of the factors affecting the levels of background herbivory at the global scale.

There exist several dozen partially overlapping or even competing hypotheses to explain the pronounced spatial and temporal variation in insect herbivory through the action of various abiotic and/or biotic factors (see, e.g., Cronin et al., 2010). One of these hypotheses, arising from the seminal works by Coley and Aide (1991) and Coley and Barone (1996), predicts a decrease in herbivory from the equator to the poles. This hypothesis had not been questioned for a long time, but a recent meta-analysis (Moles et al., 2011a) concluded that plant losses from herbivory are independent of latitude. However, several subsequent publications reported significant latitudinal decreases in herbivory in different study systems and in different geographical regions (Garibaldi et al., 2011; Kozlov et al., 2013, 2015; Więski & Pennings, 2014), and the existence of the latitudinal gradient in herbivory became the subject of heated debate. Because the idea that more herbivory occurs at lower latitudes underpins several ecological theories (Moles et al., 2011a), the identification of the reasons behind the detected variation among the outcomes of individual studies and the search for the general patterns in herbivory across latitudes world-wide are crucial for the advancement of ecology.

Climate is usually considered as the primary driver of latitudinal patterns in biotic interactions, and geographical gradients have been recently promoted as natural laboratories for studying the potential impacts of a changing climate on terrestrial organisms (De Frenne et al., 2013). The temperature gradient between the equator and poles is nonlinear: within the latitudes of 20° N and 20° S mean annual temperature shows little dependence on latitude, but outside these latitudes the slope of the temperature gradient increases towards the poles (Terborgh, 1973). In combination with latitudinal variation in the thermal sensitivities of insects (Deutsch et al., 2008), particularly expressed in the greater importance of temperatures for insects living at higher latitudes (Bale et al., 2002), this pattern hints that geographical gradients in insect herbivory at high latitudes are stronger than at low latitudes (Kozlov et al., 2013). The first empirical support for this hypothesis was found in a study of the geographical variation in losses of birch to defoliating insects and leaf miners: these losses showed no latitudinal changes between 48 and 60° N, but strongly decreased with latitude between 60 and 70° N (Kozlov, 2008). However, meta-analyses addressing latitudinal gradients in biodiversity (Hillebrand, 2004) or herbivory (Moles et al., 2011a) neither tested for the uniformity of the effect across climate zones nor controlled for this potential source of variation.

Along with climate, a latitudinal gradient in herbivory may be produced by changes in the mechanical properties of leaves (Onoda et al., 2011), in defensive chemistry (Moles et al., 2011a,b) and in predator pressure (Björkman et al., 2011). The multiplicity of factors affecting plant losses to insects, along with the diversity in the magnitudes, and even in the directions, of latitudinal patterns in herbivory reported thus far (Garibaldi et al., 2011; Moles et al., 2011a; Salazar & Marquis, 2012; Kozlov et al., 2013, 2015; Więski & Pennings, 2014), suggests that the

latitudinal patterns in herbivory may be driven by different factors in different environments. Finally, endophagous species (miners and gallers) may differ in their responses to biotic and abiotic factors from externally feeding defoliators (Castagneyrol et al., 2012; de Araújo et al., 2015), thus adding more complexity to the resulting losses of plant foliage.

The meta-analysis by Moles et al. (2011a) was based on 38 studies that reported herbivore damage to the same plant species across different latitudes. Studies of this type are relatively rare (Andrew et al., 2014), which naturally limits the statistical power of the conducted meta-analysis. The majority of the relevant scientific publications report the data on plant losses to herbivores that were collected from a single locality or from a few localities which do not form an environmental gradient. These data cannot be used in meta-analyses that address geographical variation, but they can be analysed by ordinary statistical methods to search for a latitudinal pattern. On the other hand, the published data may yield biased estimates of the levels of herbivory due to non-random selection of study objects, selective reporting of the data and their selective publication. Recently, we demonstrated that the average loss of leaf area by woody plants to defoliating insects in Brazil when estimated from blindly collected data (when the observer was not aware of the research hypothesis being tested) was significantly lower than the loss reported in studies based on non-blinded methods (Kozlov et al., 2014). To control for different forms of bias in published studies we arranged blinded collections of data on background herbivory in multiple localities across the globe and compared the results of the analyses of published and original data.

In this study we conducted a quantitative synthesis of published and original data to explore global patterns in background losses of woody plant foliage to insect herbivores. To achieve this goal, we: (1) quantified the losses of plant foliage to defoliating, leaf mining and leaf galling insects (in total and separately for each feeding guild) for different climate zones, and (2) searched for factors (related to geography and climate) which explain the variation in the levels of background herbivory across the globe. We tested the following hypotheses: (1) background herbivory generally decreases with latitude, i.e. from the equator to the poles; and (2) geographical gradients in herbivory are stronger at higher latitudes than at lower latitudes. Additionally, we checked whether the detected patterns differ among three feeding guilds of insect herbivores (defoliators, leaf miners and leaf gallers).

MATERIAL AND METHODS

Collection of published data

We searched the point data (i.e. losses measured at a single point in time) on the background damage to woody plant foliage by insects and galling mites using different databases (primarily the ISI Web of Science) and search systems (e.g. https://scholar.google.com). We used combinations of several keywords ('folivor*' or 'herbivor*', 'tree*' or 'shrub*' or 'woody', 'insect' and

'damag*' or 'loss*' or 'consum*') and examined the reference lists of the identified papers. Appendix S1 in Supporting Information gives the criteria used in the selection of papers. The search was completed on 31 October 2014.

The response variables used in this study were: (1) the percentage of leaves damaged by insects (irrespective of the extent of the damage), and (b) the percentage of leaf area (or biomass) consumed or otherwise damaged by insects (e.g. galled). The data reported by feeding guilds were not summed; the total damage (i.e. the damage imposed by all feeding guilds of insects) was included in our data set only when it was reported as such in the original publication. When the authors reported several subsequent measurements of foliar losses within a growing season in highly seasonal environments, we used the data from the last census (i.e. the damage accumulated during the entire growth season). When extracting the data from multiyear studies, we averaged the levels of herbivory for all study years. If the study involved some manipulations, we used the data from control plants. If the primary data and/or some critical information were missing, we contacted the authors for clarifications. If not provided in the publication, the coordinates of the study sites were obtained from Google Earth.

Collection of original data

The sampling protocol (Appendix S2) was developed to minimize the probability of obtaining a biased estimate of foliar damage. The collectors (ecologists who agreed to provide samples for this study) were not informed of the purpose of the sampling. Collectors were asked to sample one branch (with 100–200 leaves) from each of two haphazardly chosen individuals of each of two species of leaf-bearing woody plants which were most common in the natural ecosystems in their home areas. They were instructed to select a branch from a distance of 5–10 m (i.e. from a distance that did not allow evaluation of foliar damage). All leaves from the sampled branches (including the petioles of completely consumed leaves) were pressed between sheets of paper, dried and sent to the authors for processing. In exceptional cases (3% of samples), when sending plant material abroad required special permits, we received scanned images of the collected leaves. In highly seasonal environments, the samples were collected by the end of the growing season but before the beginning of leaf abscission.

Following a widely used methodology (Alliende, 1989), each leaf was assigned to one of the damage classes according to the percentage of the area of the leaf lamina that was consumed or damaged by insects: intact leaves, 0.01–1, 1–5, 5–25, 25–50, 50–75 and 75–100%. This assessment was conducted four times for each leaf: separately for defoliators, miners and gallers, and for the total damage imposed by all these herbivores. From each individual plant we calculated: (1) the percentages of leaves damaged by defoliators, miners, gallers and by all herbivores together (as the ratio between the number of damaged leaves and the total number of leaves in a sample multiplied by 100%); and (2) the percentages of leaf area lost to (or damaged by) insects from each of these feeding guilds and all herbivores

together. The latter values were calculated as follows: the numbers of leaves in each damage class were multiplied by the respective median value of the damaged leaf area (i.e. 0 for intact leaves, 0.5% for the damage class 0.01–1%, 3% for the damage class 1–5%, etc.); the obtained values were summed for all damage classes and divided by the total number of leaves (including undamaged ones) in a sample. Data obtained from two individual plants were averaged before further analyses.

Collection of additional information

As a rule, the names of the collected plants were provided by the collectors. Climatic data (average temperatures for January and July and annual precipitation) were obtained using New_LocClim (FAO, 2006). We interchanged July and January temperatures for studies conducted in the Southern Hemisphere to make the data comparable with studies from the Northern Hemisphere. We adopted the commonly accepted latitudinal boundaries of climate zones: tropical zone, below 23.5° (between the tropics of Cancer and Capricorn); temperate zone, from 23.5° to 66.5° (between these tropics and the polar circles); and polar zone, over 66.5° (beyond the polar circles).

Data analysis

The log-transformed percentages of the leaf area lost to (or damaged by) all feeding guilds of arthropod herbivores, as well as to defoliators, met the normality assumption, allowing the use of ANOVA (followed by the Duncan test) and regression analysis. The data on damage imposed by gallers and miners were greatly skewed due to large numbers of zeros, prompting us to use nonparametric methods (the Kruskal–Wallis test and Spearman rank correlation).

We approximated a latitudinal pattern in total losses of woody plant foliage to insects and in losses to defoliators by both linear and quadratic regressions and compared the residual variations of these models by using the Akaike information criterion (AIC). Coefficients of quadratic regression were compared between the models based on the original and published data using a *t*-test. Latitudinal patterns in damage by gallers and miners were explored by calculating Spearman rank correlation coefficients. To compare the strength of the relationships with the latitude among the climate zones and to identify factors that best explained the geographical variation, we calculated Spearman rank correlation coefficients between foliar losses, latitude and three climatic variables (temperature in January, temperature in July and annual precipitation) separately for each climate zone and for each feeding guild.

We searched for reporting and/or publication bias in the published data by calculating a Kendall τ_B correlation coefficient between the sample sizes and the reported losses to insects. Following Jennions *et al.* (2013), we presumed that if such a bias acts against small-sample studies that demonstrated unexpected levels of herbivory, then the reported foliar damage should correlate with sample size.

RESULTS

Overview of the data

We identified 309 papers (published from 1961 to 2014) that fitted our search criteria (Appendix S1). These papers reported 2122 values of the percentage of leaf area consumed or damaged by insects and 784 values of the percentage of leaves damaged by insects measured from at least 799 species of woody plants belonging to 131 families. Additionally, 150 values refer to community-wide damage measured from fallen leaves of all woody plant species present at the study sites (Appendix S3). The data originated from 698 localities across the globe (Fig. 1a) and are based on investigations of *c.* 2.5 million leaves.

Original data include 1360 values of the percentage of the leaf area consumed or damaged by insects and 1360 values of the percentage of leaves damaged by insects (Appendix S3) measured from at least 192 species of woody plants belonging to 49 families. These data originated from 147 localities (Fig. 1b) and are based on investigations of 67,695 leaves.

Average losses of plant foliage

The averaging across published and original data showed that 56.7% of the leaves bore feeding marks by insects and 7.0% of the area of woody plant foliage was eaten away or otherwise affected (mined, galled) by herbivores. The majority of damage was imposed by defoliating insects. Mines and galls were found on 5.7 and 4.4% of leaves and affected 1.0 and 0.3% of the foliage area, respectively.

At the sample-specific level, the percentage of damaged leaves strongly correlated with the percentage of the damaged leaf area (total losses: $r_S = 0.72$, $n = 765$, $P < 0.0001$). Therefore, further analyses were restricted to the percentage of removed or damaged leaf area, because this parameter better quantifies plant losses to herbivory.
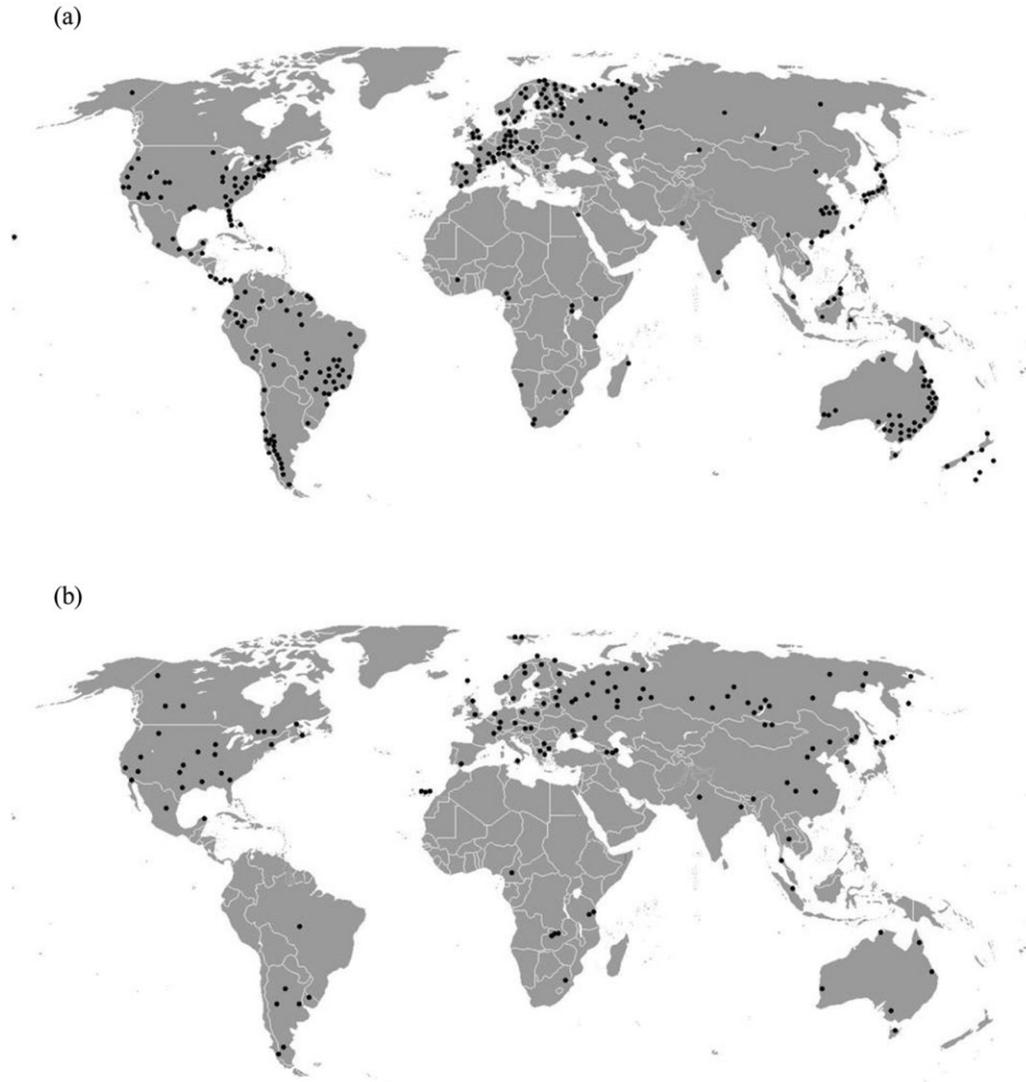

(a)

(b)

Figure 1 Locations of the sites where the data were collected: (a) published data, (b) original data.

Table 1 Comparison between published and original data on the percentage of leaf area of mature woody plants consumed or damaged by herbivores.

Herbivores	Data type	Sample characteristics					Differences between data types (d.f. = 1)	
		n	Mean	Median	Minimum	Maximum	χ^2	P
All combined	Published	1384	7.55	5.40	0	49.8	73.5	< 0.0001
	Original	337	4.73	3.02	0	36.0		
Defoliators	Published	355	7.48	6.08	0	32.0	73.8	< 0.0001
	Original	337	4.30	2.80	0	36.0		
Gallers	Published	116	0.80	0.04	0	15.3	39.7	< 0.0001
	Original	337	0.12	0	0	7.76		
Miners	Published	165	2.33	0.25	0	46.0	35.2	< 0.0001
	Original	337	0.37	0.02	0	17.3		

The published data consistently demonstrated higher levels of herbivory than the original data (Table 1). These differences remained highly significant when the data were averaged by either plant species ($P = 0.0018$) or study site ($P < 0.0001$) and when we restricted the published information to the data that were collected during a single study year ($P < 0.0001$). On average, total losses of leaf area and losses to defoliators estimated from published data were 1.6 times the respective losses measured from original samples, while published data on losses to miners and gallers exceeded the losses measured from original samples by a factor of six (Table 1). The differences between the published and original data on the total losses of plant foliage to insects were highly significant in the tropical ($F_{1, 636} = 20.4$, $P < 0.0001$) and temperate zones ($F_{1, 934} = 56.7$, $P < 0.0001$), but not in the polar zone ($F_{1, 105} = 3.03$, $P = 0.08$). Within the tropical and temperate zones, shrubs demonstrated larger differences between the published and original data in the total losses of foliage to insects (5.40 and 1.34%, respectively) than trees (5.71 and 3.74%, respectively; interaction between plant life form and the type of data, $F_{1, 1499} = 24.1$, $P < 0.0001$).

We did not find evidence for the existence of publication and/or reporting bias for either the total foliar loss or for losses to defoliators, which were independent of the number of leaves examined ($\tau_B = 0.02$, $n = 1150$, $P = 0.44$ and $\tau_B = 0.00$, $n = 304$, $P = 0.94$, respectively). However, this bias was found in the data on plant damage by gallers ($\tau_B = 0.20$, $n = 97$, $P = 0.01$) and miners ($\tau_B = -0.13$, $n = 139$, $P = 0.04$).

Geographical variation

Both the published and original data demonstrated that the total losses of woody plants to insects did not differ significantly between the tropical and temperate zones, but were significantly lower in the polar zone than in the temperate and tropical zones (Fig. 2). These differences remained highly significant when the published data were averaged by either plant species ($P = 0.0064$) or study site ($P < 0.0001$). Latitudinal changes in foliar losses were similarly expressed in the Northern and Southern Hemispheres (published data, $P = 0.13$; original data, $P = 0.88$).
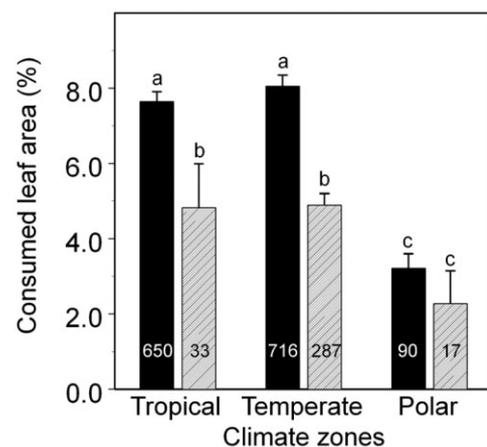

Figure 2 Variation of the total losses of woody plant foliage to insect herbivores among the climate zones: published (black bars) and original (grey bars) data (means + SE). Bars labelled with different letters differ significantly from each other (Duncan test, $P < 0.05$); sample sizes are shown within the bars.

The dome-shaped (quadratic) function of latitude explained the total losses of leaf area (Fig. 3, Table 2) significantly better than the linear function for both the original (difference in AIC = 3.59) and the published data (difference in AIC = 78.0). This pattern remained significant when the data were averaged by study site (published data, $P < 0.0001$; original data, $P = 0.0035$). Importantly, the quadratic functions fitting the original and published data differed only in an intercept (which was significantly larger in the function fitting the published data: $t = 4.05$, d.f. = 1718, $P < 0.0001$), while neither the quadratic nor the linear coefficients differed significantly ($t = 1.30$, d.f. = 1718, $P = 0.19$ and $t = 0.26$, d.f. = 1718, $P = 0.80$, respectively). This indicates that the functions fitting the original and published data differ only in the absolute levels of herbivory and not in the character of the relationships between herbivory and latitude. The damage caused by defoliators (Fig. S4, Table 2) showed similar patterns. Examination of the scatter plots (Fig. S4) suggests that the damage produced by gallers and miners also peaked in the temperate zone. However, while the original data
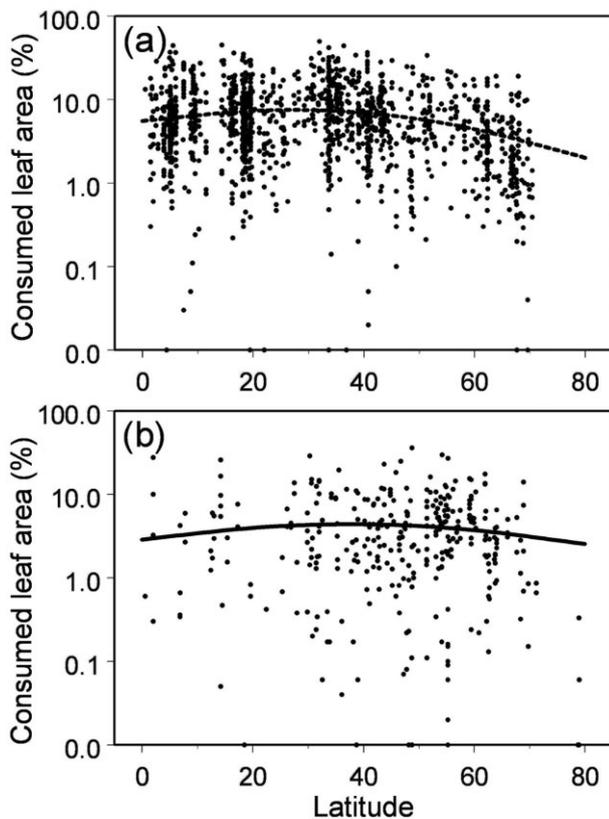
Figure 3 Geographical variation of the total losses of woody plant foliage to insect herbivores: primary data (dots) and quadratic functions of latitude (lines): (a) published data, (b) original data. See Table 2 for regression equations.

show similarly low damage at low and high latitudes, resulting in the absence of a correlation between damage and latitude (gallers, $r_S = 0.08$, $n = 338$, $P = 0.15$; miners, $r_S = 0.07$, $n = 337$, $P = 0.18$), the published data show the highest damage in the tropics, resulting in an overall poleward decrease of damage (gallers, $r_S = -0.25$, $n = 116$, $P = 0.0073$; miners, $r_S = -0.58$, $n = 165$, $P < 0.0001$).

The nonlinearity of latitudinal changes in herbivory justifies the separate analysis of the patterns observed in different climate zones. This analysis demonstrated that the total loss of leaf area and the loss to defoliators decreased with latitude in the polar and temperate zones, but not in the tropical zone, and that correlations between foliar losses and latitudes in the polar zone were stronger than in the temperate zone (Table 3). The damage imposed by gallers increased with latitude in the temperate zone, but showed no latitudinal patterns in either the polar or tropical zones (Table 3). Damage imposed by miners decreased with latitude in the tropical zone, but showed no latitudinal patterns in either the polar or temperate zones (Table 3).

The relationships between the losses of leaf area and the investigated climatic variables also varied among the climate zones and among the feeding guilds of insects (Table 3). The total loss of leaf area in the polar zone was best explained by the midsummer temperature and in the temperate zone by the midwinter temperature, while in the tropical zone it was independent of climate. The losses to defoliators in all climate zones were best explained by precipitation. The damage by gallers showed little correlation with climatic variables. The damage by miners in the polar zone was best explained by midwinter temperatures, while in the temperate zone and especially in the tropical zone it strongly increased with precipitation (Table 3).

DISCUSSION

Levels of plant damage

Our data set includes 3482 point estimates of the percentage of leaf area consumed or damaged by arthropod herbivores, primarily insects. These data were collected from at least 941 species of woody plants (the number of investigated plant species is obviously higher, because some species were identified to genus level or were not identified) from 136 families in 836 localities from equator to as close to a pole as 78°56′ N. This data set, in terms of woody plants, is several times larger than one recently published by Turcotte et al. (2014a,b) and was collected using selection criteria and approaches which differ from those used by those authors. In particular, we excluded the data that could confound latitudinal patterns, for example those collected during outbreaks of eruptive species and from juvenile plants. Finally, our data set is exceptional in the coverage of latitudes: 45% of the earlier studies reporting latitudinal patterns in herbivory that were considered in the meta-analysis by Moles et al. (2011a) were conducted in geographical gradients that did not exceed 10° of latitude, and 27% of the gradients were between 10° and 15° of latitude.

Our focus on woody plants is justified by their importance for the global carbon cycle: forests hold 70–90% of terrestrial biomass, most of it in trees (Houghton et al., 2009). The losses of woody plant foliage to herbivorous insects obtained in our study are significantly lower than the previously reported (e.g. Cyr & Pace, 1993; Coley & Barone, 1996) levels of herbivory in terrestrial ecosystems, especially in forests, but fall into the same range as the estimates for different groups of woody plants provided by Turcotte et al. (2014b).

The levels of herbivory calculated from original data were significantly lower than those calculated from published data. We did not find publication bias in the total loss of plant foliage, and therefore attribute the discovered differences to a research bias in the published studies, expressed in the unconscious selection of species showing higher than average levels of foliar losses (Kozlov et al., 2014). The existence of this bias was indirectly confirmed by the finding that shrubs demonstrated much larger differences between the published and original data in the total losses of foliage to insects than trees, probably because for trees the chances of the biased selection of branches with higher than average foliar damage are lower than in shrubs, in which the entire canopy can be unintentionally accessed by the collector. We exerted every effort to collect our original data blindly. Therefore our results suggest that the research bias leading to

Table 2 Regression of the percentages of leaf area of mature woody plants consumed by herbivores [values transformed as $\ln(1 + x)$] on latitude for published and original data.

Regression model	Plant losses	Data type	Parameter estimates (mean ± SE)			Model characteristics			
			Intercept	Latitude ($\times 10^3$)	Latitude^2 ($\times 10^4$)	R^2	F	P	AIC
Linear	Total loss	Published	2.05 ± 0.04	−9.90 ± 1.03	–	0.031	44.5	< 0.0001	−683.2
		Original	1.47 ± 0.14	−1.49 ± 2.85	–	0.001	0.27	0.60	−124.8
	Loss to defoliators	Published	2.34 ± 0.07	−13.8 ± 1.80	–	0.136	55.9	< 0.0001	−218.3
		Original	1.47 ± 0.14	−2.93 ± 2.80	–	0.003	1.09	0.30	−137.4
Quadratic	Total loss	Published	1.68 ± 0.06	27.2 ± 3.90	−4.98 ± 0.55	0.086	64.7	0.0001	−761.3
		Original	1.04 ± 0.23	24.7 ± 11.3	−3.28 ± 1.37	0.018	3.01	0.05	−128.5
	Loss to defoliators	Published	2.14 ± 0.09	4.72 ± 5.74	−2.72 ± 0.80	0.164	34.6	< 0.0001	−227.7
		Original	1.10 ± 0.22	19.3 ± 11.2	−2.79 ± 1.35	0.016	2.68	0.07	−139.7

Table 3 Spearman rank correlations (r_S / P-values) between the percentage of leaf area of mature woody plants consumed or damaged by herbivores and characteristics of the study sites.

Herbivores	Climate zone	Sample size	Characteristics of study sites			
			Latitude	T1*	T2†	Precipitation
All combined	Polar	107	−0.36 / 0.0001	−0.13 / 0.17	0.35 / 0.0002	0.21 / 0.03
	Temperate	936	−0.22 / 0.0001	0.19 / 0.0001	0.01 / 0.82	0.13 / 0.0001
	Tropical	678	0.05 / 0.19	0.03 / 0.45	0.06 / 0.10	−0.03 / 0.43
Defoliators	Polar	51	−0.40 / 0.0041	0.04 / 0.76	0.38 / 0.006	0.54 / 0.0001
	Temperate	518	−0.21 / 0.0001	0.20 / 0.0001	0.17 / 0.0001	0.23 / 0.0001
	Tropical	125	−0.18 / 0.05	−0.05 / 0.59	0.07 / 0.42	0.27 / 0.002
Gallers	Polar	44	0.24 / 0.12	0.10 / 0.52	−0.30 / 0.05	−0.11 / 0.49
	Temperate	366	0.15 / 0.0051	−0.06 / 0.24	0.01 / 0.78	0.12 / 0.02
	Tropical	44	0.03 / 0.85	0.13 / 0.40	−0.19 / 0.23	0.10 / 0.54
Miners	Polar	45	−0.11 / 0.45	0.30 / 0.05	−0.04 / 0.80	0.13 / 0.39
	Temperate	386	−0.06 / 0.21	0.16 / 0.0018	0.19 / 0.0002	0.22 / 0.0001
	Tropical	71	−0.24 / 0.05	0.30 / 0.01	−0.01 / 0.90	0.51 / 0.0001

*T1, mean temperature in January for the localities in the Northern Hemisphere and in July for the localities in the Southern Hemisphere.
†T2, mean temperature in July for the localities in the Northern Hemisphere and in January for the localities in the Southern Hemisphere.

overestimation of herbivory levels is not restricted to the tropics but occurs globally, although the comparison between the original and published data (Fig. 2) suggests that this bias tends to be highest in the tropical zone.

The differences between the published and original data were largest for miners and gallers (Table 1), possibly because plant losses to these herbivores were explored only when their occurrence was well manifested. Damage by miners and gallers could also be underreported when the obtained values were rather small and therefore considered 'negligible', as indicated by significant correlations between sample size and the reported level of damage. Some researchers (e.g., Oliveira *et al.*, 2012) honestly mentioned that mines and/or galls were rare and therefore their occurrence had not been measured. The shortage of published information on plant losses to miners and gallers calls for measuring and reporting these losses – even when they approach zero or are equal to zero – in order to clarify the patterns in plant damage imposed by these specialized herbivores.

Geographic variation in background herbivory

Latitudinal patterns in the different characteristics of ecosystems have fascinated biologists for centuries. While an increase in species richness from the poles towards the equator is now seen as a general pattern (Hillebrand, 2004), our understanding of latitudinal patterns in biotic interactions, including herbivory, is still controversial (Schemske *et al.*, 2009). Resolving this controversy will have important implications for the development of basic ecology. Variations in the pressure which herbivores impose on plants serve as the cornerstone for numerous hypotheses/theories related to insect–plant relationships, such as the 'green world' hypothesis (Hairston *et al.*, 1960; Polis, 1999), the exploitation ecosystem hypothesis (Oksanen *et al.*, 1981; Polis, 1999), the optimal defence theory (Rhoades, 1979) and many others, as well as for theories explaining the evolution of plant traits (Coley & Aide, 1991) and the formation of biogeographical patterns (Moles *et al.*, 2011a).

Springett (1978) was probably the first to compare foliar losses measured in different geographical regions. He concluded that plant damage was essentially similar between tropical rain forests and northern temperate forests, and our results (Fig. 2) confirm this conclusion. Landsberg and Ohmart (1989) also found identical levels of background herbivory in temperate forests, rain forests and mangrove forests. In contrast, Coley and Aide (1991) and Coley and Barone (1996), by summarizing the outcomes of 17 and 23 case studies, respectively, concluded that plant damage by insect herbivores in tropical forests was higher than in temperate forests. The two latter publications are widely cited as evidence for a latitudinal gradient in herbivory because this pattern fits a number of theoretical assumptions well (reviewed by Adams & Zhang, 2009; Moles *et al.*, 2011a,b; Rasmann & Agrawal, 2011). Importantly, although our results agree with the general conclusion by Coley and Aide (1991) and Coley and Barone (1996) on the existence of a latitudinal gradient in herbivory, we did not confirm their particular conclusion about higher levels of herbivory in the tropics compared with the temperate zone.

Our study based on extensive data not only provided solid support for the hypothesis on the decrease in background herbivory with latitude (at least outside the tropics), but for the first time also demonstrated that this latitudinal gradient is nonlinear, i.e. its slope differs between the climate zones. The background insect herbivory is independent of latitude within the tropical zone, slightly decreases with latitude in the temperate zone and strongly decreases with latitude both between the temperate and polar zones and within the polar zone. This pattern is consistent with the poleward increase in the slope of the temperature gradient (Terborgh, 1973) and with the greater importance of temperature rise for insects living in polar climates relative to insects in temperate regions (Bale *et al.*, 2002; Deutsch *et al.*, 2008). Importantly, despite the differences found between the mean values, the published and original data produced uniform results with respect to geographical variation. Furthermore, our data suggest that factors explaining the latitudinal patterns in background herbivory differ between the climate zones. In particular, the total loss of leaf area in the polar zone was best explained by midsummer temperatures, and this result agrees with our earlier finding that midsummer temperatures best explain plant losses to defoliators, leaf miners and sap-feeders in boreal forests (Kozlov, 2008; Kozlov *et al.*, 2013, 2015). Plant losses in the temperate zone were best explained by midwinter temperatures, confirming the conclusion (Bale *et al.*, 2002) that in temperate regions temperature primarily affects insects through their winter survival. Finally, in the tropical zone, herbivory was independent of either latitude or climate, which agrees with the small dependence of temperatures on latitudes within 20° of the equator (Terborgh, 1973).

Among the herbivore feeding guilds, gallers appeared most independent of either latitude or climate. This independence is in line with the exceptional pattern of species richness in gallers, which peaks in warm temperate latitudes (Price *et al.*, 1998), whereas the diversity of most taxa monotonously decreases with latitude (Hillebrand, 2004). The absence of a latitudinal gradient in foliar damage by gallers is possibly related to their ability to manipulate host plant tissues to their own advantage, which decreases their dependence on the abiotic environment (Hartley & Lawton, 1992).

The positive correlation between herbivory and precipitation discovered in our study is difficult to explain, because earlier studies reported either the absence of a precipitation effect on leaf damage by insects (Vasconcelos, 1999) or higher herbivory in dry forests relative to wet forests (Mazía *et al.*, 2012). The effects of precipitation have been largely neglected in current research on climate change in general (Bale *et al.*, 2002) and on the effects of climate on herbivory in particular. Our results indicate that precipitation may have diverse and yet unpredictable impacts on insect–plant relationships.

Conclusions

Both published and original data, despite the significant difference in mean losses to insects, consistently demonstrated that the background herbivory changes with latitude and that this change is nonlinear. Losses of woody plant foliage to insect herbivores showed a dome-shaped latitudinal pattern: peaking in the temperate zone, slightly decreasing towards the equator and strongly decreasing towards the poles. The climatic factors explaining latitudinal patterns in background herbivory are likely to differ among the climate zones. Although the positive correlation between temperatures and herbivory in regions with temperate to cold climates cannot be taken as a proof of functional dependence, our finding is in line with the commonly accepted opinion that insects living at higher latitudes are generally controlled by temperatures. All these data suggest that climate warming is likely to result in an increase in the background herbivory outside the tropics, and that this increase in the polar zones will be higher than in temperate zones.

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Additional references to the sources of data used in this study can be found in Appendix S1 in the Supporting Information.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Criteria used in the selection of papers, and the list of selected papers.
Appendix S2 Sampling protocol.
Appendix S3 Damage of woody plant leaves by herbivorous insects.
Appendix S4 Percentage of leaf area of mature woody plants consumed or damaged by herbivores from different feeding guilds plotted against latitude

BIOSKETCHES

Mikhail V. Kozlov is interested in the evolutionary ecology of insect–plant relationships and in the effects of environmental stressors, primarily industrial pollutants, on the structure and functions of terrestrial ecosystems. The current research of his team focuses on global patterns in levels of background herbivory and on the responses of plants to herbivore damage. The team uses holistic approaches for solving ecological problems by combining field observations, manipulative studies and meta-analyses.

M.V.K. and E.L.Z. designed the research; M.V.K., V.L., V.Z. and E.L.Z. performed the research; M.V.K. analysed the data; M.V.K. and E.L.Z. wrote the first draft of the manuscript; all authors contributed substantially to revisions.

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