

SYNTHESIS

Latitudinal gradient in the intensity of biotic interactions in terrestrial ecosystems: Sources of variation and differences from the diversity gradient revealed by meta-analysis

Elena L. Zvereva  | Mikhail V. Kozlov 

Department of Biology, University of Turku, Turku, Finland

CorrespondenceElena L. Zvereva, Department of Biology, University of Turku, FI-20014, Turku, Finland.
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Abstract

The Latitudinal Biotic Interaction Hypothesis (LBIH) states that the intensity of biotic interactions increases from high to low latitudes. This hypothesis, which may partly explain latitudinal gradients in biodiversity, remains hotly debated, largely due to variable outcomes of published studies. We used meta-analysis to identify the scope of the LBIH in terrestrial ecosystems. For this purpose, we explored the sources of variation in the strength of latitudinal changes in herbivory, carnivory and parasitism (119 publications) and compared these gradients with gradients in the diversity of the respective groups of animals (102 publications). Overall, both herbivory and carnivory decreased towards the poles, while parasitism increased. The latitudinal gradient in herbivory and carnivory was threefold stronger above 50–60° than at lower latitudes and was significant due to interactions involving ectothermic consumers, studies using standardised prey (i.e. prey lacking local anti-predator adaptations) and studies aimed at testing LBIH. The poleward decrease in biodiversity did not differ between ectothermic and endothermic animals or among climate zones and was fourfold stronger than decrease in herbivory and carnivory. The discovered differences between the gradients in biotic interactions and biodiversity suggest that these two global macroecological patterns are likely shaped by different factors.

KEYWORDS

biodiversity, biotic interactions, herbivory, latitudinal gradient, macroecology, meta-analysis, parasitism, predation, terrestrial ecosystems, thermoregulation strategy

INTRODUCTION

The global decrease in biodiversity from low to high latitudes is so ubiquitous that this pattern is seen as one of the fundamental ecological laws (Lawton, 1999). Nevertheless, the reasons behind the latitudinal biodiversity gradient remain debatable (Currie et al., 2004;

Kinlock et al., 2018; Willig et al., 2003). One of several hypotheses raised to explain this fascinating pattern associates the biodiversity gradient with a latitudinal gradient in the intensity of biotic interactions (Pianka, 1966; Rohde, 1992; Schemske et al., 2009). According to the Latitudinal Biotic Interaction Hypothesis (LBIH), the importance of biotic interactions is greater in benign

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tropical environments than it is at higher latitudes, where abiotic factors play the leading role in shaping biotic communities (Dobzhansky, 1950; Fischer, 1960; Schemske et al., 2009).

The occurrence of a latitudinal gradient in biodiversity is supported by an enormous number of studies on various taxonomic groups; the accumulated data are now summarised in multiple narrative reviews (e.g. Currie et al., 2004; Willig et al., 2003) and in two meta-analyses (Hillebrand, 2004; Kinlock et al., 2018). Conversely, support for the existence of a similar gradient in the intensity of biotic interactions has been mixed (Anstett et al., 2016; Moles et al., 2011). The LBIH has recently become a subject of heated debate due to the highly variable outcomes of published studies, and it was even called ‘a zombie idea’ (Moles & Ollerton, 2016). Despite the large number of studies, a poleward decrease in the intensity of biotic interactions as a general macroecological pattern remains in question.

The previous meta-analysis by Moles et al. (2011) did not support the LBIH for herbivory, but the relatively low number of publications available at that time (38) hampered detailed deciphering of sources of variation among studies. Nevertheless, several factors have been suggested to explain this variation (Andrew et al., 2012; Anstett et al., 2016; Carmona et al., 2020; Dyer & Forister, 2019). They include differences in sampling design, such as the use of gradients or contrasts between latitudes (Anstett et al., 2016), the use of gradients located between and within climate zones or biomes (Dyer & Forister, 2019; Marquis et al., 2012), the origin of data from different hemispheres (Scholer et al., 2020; Zhang et al., 2016) and the assessment of interactions in individual systems or at the level of entire communities (Anstett et al., 2016; Zvereva et al., 2020a), as well as the assessment of interactions using standardised or natural prey (Chen & Moles, 2018; McKinnon et al., 2010). Variation in the latitudinal patterns of biotic interactions was also explained by differences between predation and parasitism (Hawkins et al., 1997; Zvereva et al., 2020b) and between invertebrate and vertebrate (or ectothermic and endothermic) predators (Peco et al., 2014; Roslin et al., 2017; Zvereva et al., 2019) and herbivore feeding guilds (Andrew et al., 2012; Carmona et al., 2020). Testing for generality of existing explanations for the variation in the outcomes of the currently available studies requires quantitative research synthesis. We focussed this synthesis on the most important trophic interactions: herbivory, predation and parasitism. The number of publications addressing latitudinal patterns in these interactions is sufficient for quantifying both the general pattern and the sources of variation among individual studies.

Any theory usually goes through three stages of development: the prevalence of supportive evidence in early tests of the newly formulated hypothesis, the accumulation of disconfirming evidence and, finally, a

reformulation of the original hypothesis, leading to restriction of its scope (Leimu & Koricheva, 2004). The LBIH has received considerable amounts of both supportive and disconfirming evidence and is thus likely approaching the third stage. We suggest that quantitative analysis of multiple sources of variation among the outcomes of latitudinal studies would contribute to theory maturation (as defined by Loehle, 1987) by identifying the scope and the applicability limits of the LBIH.

Latitudinal changes in the intensity of biotic interactions have been considered both as a cause and as a consequence of the latitudinal biodiversity gradient (Pianka, 1966; Rohde, 1992; Schemske et al., 2009). Nevertheless, we are not aware of any attempt to directly compare these two global gradients, although this type of comparison would aid in resolving the long-standing question about the association between macroecological patterns in biodiversity and in biotic interactions. Meta-analysis is a perfect tool for tackling this challenge with the existing data and for comparing the basic characteristics of these global gradients because it can provide a synthesis of the outcomes of the wealth of studies. The two published meta-analyses of biodiversity gradients (Hillebrand, 2004; Kinlock et al., 2018) make diversity data readily available for this kind of comparison.

The first goal of our present study was to identify the scope and uncover applicability limits of the LBIH by quantifying both the general pattern in latitudinal changes in herbivory, predation and parasitism in terrestrial ecosystems and the sources of variation among the outcomes of individual studies. Our second goal was to explore effects of biases, defined as systematic errors in results or inferences that favour one outcome over others, on studies addressing the LBIH. The analysis of and accounting for publication and confirmation biases, which are widespread in ecological research (Holman et al., 2015; Jennions et al., 2013; Zvereva & Kozlov, 2019), would aid arriving at unbiased conclusions, despite some part of published data may be biased. Our third goal was to compare the strength and sources of variation between latitudinal gradients in biotic interactions and in the diversity of organisms involved in these interactions, as this would clarify any association between these two macroecological gradients and/or their likely abiotic drivers. Based on previous studies, we proposed the following hypotheses:

1. The intensity of biotic interactions decreases from the equator to the poles.
2. This decrease is similarly expressed in different trophic interactions (herbivory, carnivory and parasitism).
3. Latitudinal changes in the intensity of biotic interactions depend on the thermoregulation strategy of the involved organisms.
4. The strength of the latitudinal gradient in biotic interactions differs between climate zones.

5. Latitudinal changes in the intensity of biotic interactions are strongest between tropical and temperate zones.
6. The strength of the latitudinal gradient in biotic interactions differs between both Northern versus Southern and Eastern versus Western hemispheres.
7. The latitudinal changes in herbivory/carnivory on standardised plant/prey are stronger than on local plant/prey due to their pre-existing anti-predator adaptations.
8. Publication bias favours studies that support the LBIH.
9. Latitudinal changes in biotic interactions and in biodiversity follow similar patterns in terms of both the sources of variation and the magnitude of the effect.

We tested these hypotheses by meta-analyses of the outcomes of 119 publications reporting latitudinal changes in herbivory, carnivory and parasitism in terrestrial ecosystems and of 102 publications reporting latitudinal changes in the diversity of the animals involved in these interactions.

MATERIALS AND METHODS

General approach

We focussed our meta-analysis on interactions that are broadly defined as predation (i.e. as consumption of one organism by another organism: Krebs, 2013; Smith & Smith, 2015). These interactions are conventionally classified into herbivory, carnivory and parasitism (Krebs, 2013) and are sufficiently studied across the globe (Schemske et al., 2009) to justify an attempt at meta-analysis of their latitudinal changes. We classified as parasites those organisms which live on or in their hosts for some part of their life cycle (Smith & Smith, 2015). We classified animals, which consume animal tissues, as carnivores, and animals that consume plant tissues as herbivores (Krebs, 2013; Smith & Smith, 2015). Although some herbivores (leaf miners and gall makers) fit the definition of parasites, we follow the traditional approach and include all plant-eating organisms in the herbivore category. In a functional classification, the term 'predator' or 'true predator' is used for carnivores that kill their prey immediately upon capture, whereas herbivores generally consume only a part of an individual plant. We classified seed-eating animals as herbivores based on the organisms consumed, although they function as true predators.

We extracted information from studies (both primary and combining published data) that fit the following criteria: (i) the data were collected from natural ecosystems, (ii) the data were collected from at least two study sites located at least two degrees of latitude apart and (iii) the magnitude of the effect was available from the study or

could be calculated from the data or statistics presented in the publication or provided by authors.

Search for and processing of studies on biotic interactions

We identified suitable studies based on earlier reviews of latitudinal changes in biotic interactions (Anstett et al., 2016; Moles et al., 2011; Schemske et al., 2009), and we searched for additional publications in the ISI Web of Science using the keywords 'latitud*', 'geographic', 'biotic interactions', 'herbivor*', 'predat*', 'carnivor*' and 'parasit*'. The search was completed in December 2020. We included only studies that contained direct quantitative estimates of the intensity of herbivory (the percentage of plant biomass or leaf area lost to herbivores or the proportion of damaged leaves), carnivory (the mortality of prey or the predator attack rates) or parasitism (prevalence; i.e. percentage of infected hosts). We rejected studies where the interaction intensity was deduced from the abundance of herbivores/predators and where interactions could have been affected by human activities, such as herbivory by semi-domesticated reindeer or by large animals whose numbers have considerably decreased over the past decades due to human-induced changes in vegetation (e.g. in the savannah: Jia et al., 2018; Young et al., 2013).

The vast majority of studies exploring latitudinal patterns in biotic interactions employed sites located at about the same (usually low) elevations. If elevation varied greatly within a study, we removed sites with deviating elevations from effect size calculations to prevent their undue influence on latitudinal pattern. When a study reported data collected over several years, we selected the year with the highest number of sites (e.g. Kelly et al., 2008) or with the longest latitudinal gradient (e.g. Bensch & Åkesson, 2003). However, if data from different years were pooled by the authors (e.g. Zvereva et al., 2020b), then we used the pooled data. When a study reported data collected from multiple localities from two or three climate zones (Hargreaves et al., 2019; Kozlov et al., 2015; Peco et al., 2014; Zhang et al., 2016), we divided these data by climate zones and then by continents. Entire global gradients were excluded from the analyses when our focus was on gradients either located within one climate zone or crossing a border between the two adjacent zones.

Search for and processing of studies on diversity

The larger part of the data on latitudinal changes in terrestrial biodiversity was directly extracted from the published databases (Hillebrand, 2004; Kinlock et al., 2018), resulting in 166 effect sizes (ES, hereafter) for taxonomic groups involving herbivorous, carnivorous and omnivorous animals. However, studies conducted at

high latitudes were underrepresented in these databases compared with our database on biotic interactions. This prompted us to search for additional studies from sub-arctic and arctic regions in the Web of Science and in eLibrary.ru (published in English and Russian, respectively) using the keywords 'latitud*', 'diversity', 'polar', 'arctic', 'tundra' and 'boreal'. This search yielded 17 publications, from which we calculated 32 ES by the method used by Hillebrand (2004) and Kinlock et al., (2018). In combination with data from previously published meta-analyses, this yielded 198 ES.

Classificatory variables

Biotic interactions were classified into herbivory, carnivory and parasitism as described above. Organisms involved in these interactions were divided into ectotherms (invertebrates and reptiles) and endotherms (birds and mammals); for parasites, we applied this classification to their hosts. Herbivory was divided into defoliating, mining, galling, sap-feeding, seed predation and mammalian grazing. The term 'folivory' was used for studies that measured overall leaf damage, usually combining damage imposed by defoliators and miners. We also classified host plants and prey into natural, permanently inhabiting the study areas, and standardised (both live and artificial); the latter were introduced to all study sites by the researchers and therefore lacked local adaptations to predators.

From the geographical perspective, the data were attributed to hemispheres (both Western/Eastern and Northern/Southern) and to continents. Within continents, all gradients were classified as located entirely within a single climate zone, as running across two adjacent climate zones, or as global and passing through all three climate zones (tropical, temperate and polar). The boreal forests were included in the polar zone. Due to variation in the latitudinal positions of the borders between tropical, temperate and boreal forests, the attribution of study sites to climate zones was based on data provided in the original publications.

We divided all studies into two groups: studies based on original data and studies analysing published data from different latitudes. Finally, we classified all publications into those aimed and not aimed at testing the LBIH. The latter included both non-hypothesis-driven studies and studies testing some other hypotheses. The visibility of journals in which the studies were published was quantified by their impact factors (IF hereafter; obtained from the ISI Web of Sciences) for the year 2018. For publications lacking IF, we arbitrarily accepted $IF = 0$.

Meta-analysis

We quantified the strength of the latitudinal gradients by the z -transformed correlation between latitude and

the intensity of the interactions (z_r), similar to previously published meta-analyses of the diversity data (Hillebrand, 2004; Kinlock et al., 2018). We used two approaches for the ES calculation. When a study compared a measure of biotic interactions among a limited number of sites, which often did not form a latitudinal gradient in the strict sense, we calculated Hedge's d from the differences between the two sites (or groups of sites) with extreme latitudes and converted d into a z_r value using a web calculator (www.psychometrica.de/effect_size.html). When a study reported the correlation between the strength of a biotic interaction and latitude, we converted the correlation coefficient into a z_r value. The ES calculated by these two methods for 23 randomly selected studies (Table SM1 in Zvereva & Kozlov, 2021b) did not differ from each other (from correlation coefficients: $z_r = -0.39$, CI_{95} from -1.58 to -0.20 ; from contrasts between the ends of this gradient: $z_r = -0.48$, CI_{95} from -0.67 to -0.29 ; $Q_B = 0.52$, $df = 1$, $p = 0.49$), thereby justifying combination of ES calculated by these two methods in our analyses.

To compare z_r among different groups of studies, we calculated the between-group heterogeneity (Q_B) using a random effects model, and we tested Q_B against the χ^2 distribution with the number of groups minus one degree of freedom (Koricheva et al., 2013). We explored the latitudinal changes in z_r by means of a meta-regression to the midpoints of the studied gradients (calculated following Kinlock et al., 2018; except for gradients that crossed the equator). We also used meta-regression to check whether ES depends on the extension of the gradient, journal impact factor or from a publication year, and we searched for publication bias by calculating the Kendall τ correlation between the standardised ES and sample size (Rosenberg et al., 2000); the significant correlation was interpreted as the presence of a small study effect hinting at publication bias (Jennions et al., 2013). Finally, we calculated Rosenthal's fail-safe number, which shows the number of insignificant studies that are required to turn the significant mean ES into an insignificant one. The fail-safe numbers exceeding $5n$ (where n is the number of studies included in the meta-analysis) are considered as proof that the analysis is robust against the insignificant results (Møller & Jennions, 2001; Rosenthal, 1979).

RESULTS

Overview of the data and general latitudinal pattern in biotic interactions

We discovered 119 publications (dated from 1979 to 2020) that satisfied our criteria, and we calculated 317 ES, including 232 ES based on original studies and 85 ES based on studies that combined published data to explore latitudinal changes (Table SM2 in Zvereva & Kozlov, 2021b). The data were dominated by studies of

herbivory (68.7% of ESs) on vegetative (leaves, stems) and generative organs (seeds, flowers) of vascular plants. The data on carnivory (18.6%) reflected primarily predation on natural and artificial bird nest and insect prey. The data on parasitism (12.6%) involved both external and internal parasites of vertebrates and parasitoids of insects.

Of 317 ES, 101 were based on contrasts between sites (or groups of sites) located at different latitudes, while the remaining 216 were based on correlations with latitude. The number of sites in correlation studies ranked from 4 to 280 (median value: 17 sites). Geographically, the identified studies covered latitudes from the equator to 83°N and 55°S and all continents (Figure 1a; Europe: 108 ES; North America: 91 ES, South America: 21 ES; Asia: 21 ES; Australia: 18 ES; Africa 6 ES); 52 ES combined data from two or more continents and therefore could not be depicted on the map. The extension of gradients (or distance between extreme sites) varied from 2 to 120 degrees of latitude (median value: 14 degrees of latitude).

The intensity of biotic interactions generally decreased with latitude (Figure 1b), and this pattern was robust against unpublished studies (the Rosenthal's fail-safe number equals $7.3n$, i.e. 7.3 times greater than the number of studies included in our meta-analysis).

Variation associated with the organisms involved

Types of biotic interactions

The studied biotic interactions significantly differed in their relationship with latitude (Figure 1b; $Q_B = 16.2$, $df = 2$, $p = 0.0003$). This difference was due to the

poleward increase in parasitism, while herbivory and carnivory similarly ($Q_B = 0.02$, $df = 1$, $p = 0.89$) decreased from the equator to the poles (Figure 1b). The Rosenthal's fail-safe number for herbivory combined with carnivory was $13n$, whereas for parasitism, it was smaller than the number of studies included in meta-analysis.

Within herbivory, the damage caused by most guilds of insect leaf-eaters significantly decreased with the increase in latitude, while damage caused by gall-forming invertebrates, mammalian herbivores (grazers) and seed predators did not demonstrate any latitudinal changes (Figure 2). Infestation by insect parasitoids significantly increased with latitude ($z_r = 0.39$, CI_{95} from 0.07 to 0.72, $n = 8$) and did not differ from latitudinal changes in prevalence of true parasites ($Q_B = 1.93$, $df = 1$, $p = 0.16$).

Thermoregulation strategies of interacting organisms

The pressure of ectothermic animals on lower trophic levels demonstrated a significantly stronger relationship with latitude than did the pressure of endotherms (Figure 3); this difference was found for both herbivores ($Q_B = 4.36$, $df = 1$, $p = 0.04$) and carnivores ($Q_B = 25.8$, $df = 1$, $p < 0.0001$). Plant losses to endothermic herbivores and pressure by endothermic carnivores on their prey did not correlate with latitude (Figure 3). Parasitism on ectothermic hosts showed a threefold stronger positive correlation with latitude than was observed for parasitism on endothermic hosts (Figure 3), although this difference was not significant ($Q_B = 0.78$, $df = 1$, $p = 0.37$) due to relatively low number of studies addressing latitudinal variation in parasitism.

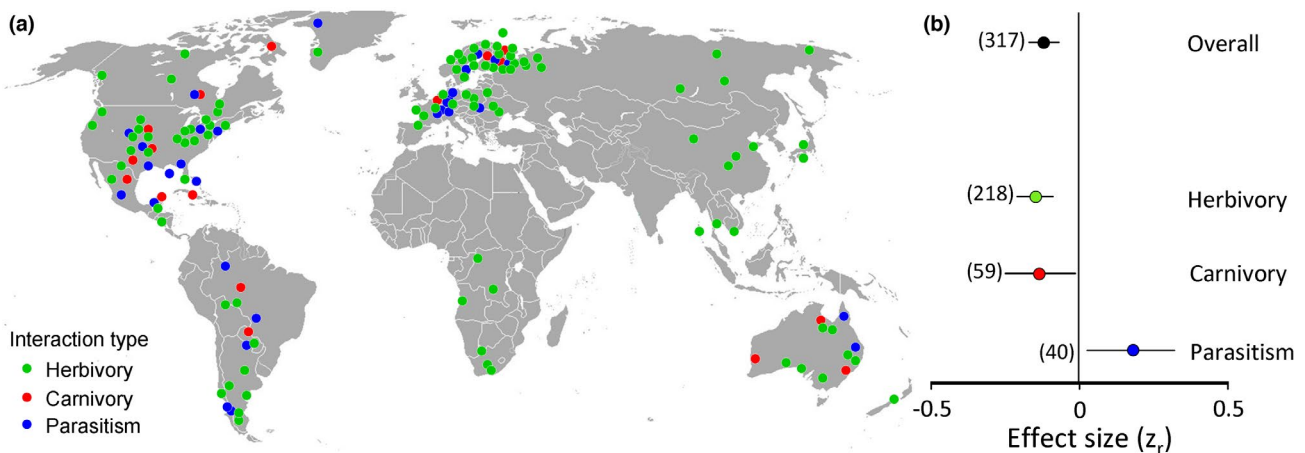


FIGURE 1 The approximate positions of the midpoints of the latitudinal gradients and contrasts between sites from different latitudes in herbivory, carnivory and parasitism (a) and strength of latitudinal changes in the intensity of these interactions (b). On the map, gradients and contrasts involving more than one continent are not shown; each dot may include several effect sizes calculated from the same gradient/contrast. On the graph, the negative effect size indicates a decrease in the interaction intensity with an increase in latitude. Horizontal lines denote 95% confidence intervals; numbers of effect sizes are shown in parentheses. For statistical analysis, see text

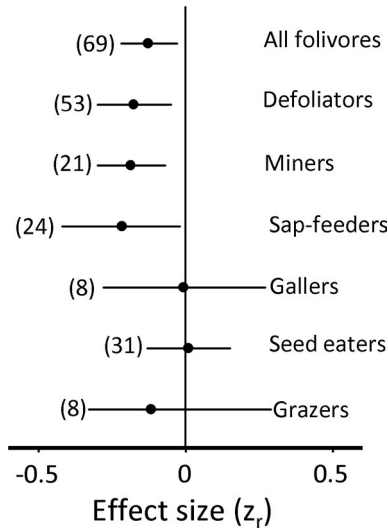


FIGURE 2 The strength of latitudinal changes in the intensity of plant damage imposed by different guilds of herbivores. ‘All folivores’ refer to studies which do not distinguish foliar damage between insect feeding guilds. For other explanations, refer to Figure 1; for statistical analysis, see text

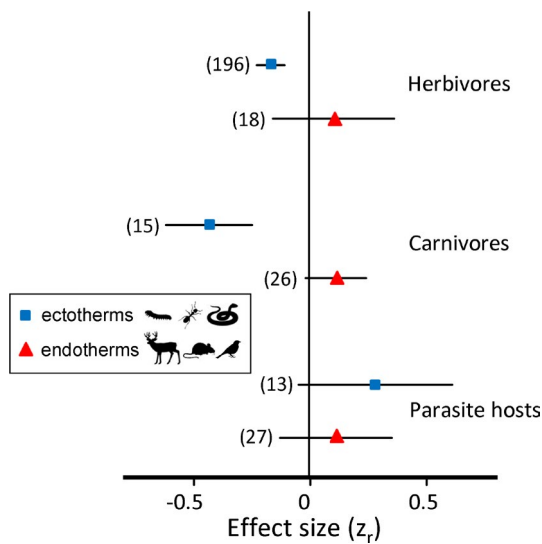


FIGURE 3 The strength of latitudinal changes in the intensity of herbivory, carnivory and parasitism in relation to thermoregulation strategy of herbivores, carnivores and hosts of parasites. For explanations, refer Figure 1; for statistical analysis, see text

Variation associated with geographical factors

Differences between hemispheres and continents

The correlation between the intensity of biotic interactions and latitude did not differ between Western and Eastern hemispheres for either herbivory combined with carnivory (Figure 4; $Q_B = 1.02$, $df = 1$, $p = 0.31$) or parasitism ($Q_B = 0.88$, $df = 1$, $p = 0.35$). Correlation of herbivory and carnivory with latitude was twice stronger in Northern than in Southern hemisphere (Figure 4; $Q_B = 1.71$, $df = 1$, $p = 0.19$), but this difference disappeared

when we excluded from the analysis high latitudes, for which no data exist from terrestrial ecosystems of the Southern hemisphere (Figure 4; $Q_B = 0.14$, $df = 1$, $p = 0.70$). Latitudinal changes in parasitism did not differ between Northern and Southern hemispheres ($Q_B = 2.01$, $df = 1$, $p = 0.16$), but the low number of studies from the Southern hemisphere ($n = 6$) makes this result tentative. Differences among continents were non-significant for both low (tropical and temperate) latitudes ($Q_B = 4.25$, $df = 5$, $p = 0.51$) and high (polar) latitudes ($Q_B = 0.52$, $df = 3$, $p = 0.91$).

Latitudinal changes in the strength of correlation

For herbivory combined with carnivory, the difference between all gradients located within a single climate zone and all gradients spreading to more than one zone was not significant ($Q_B = 0.41$, $df = 1$, $p = 0.52$). When we classified ES into five groups, three of which reflect latitudinal differences within a single climate zone and two of which include the border between the two adjacent zones, the correlations between the intensity of herbivory plus carnivory and latitude significantly varied among these groups of ES (Figure 5; $Q_B = 15.1$, $df = 4$, $p = 0.005$). These correlations were not significant for gradients located within tropical and temperate zones but they were significant for the gradients that ran through both the tropical and temperate zones (Figure 5). However, the fail-safe number for the latter gradient was low ($1.4n$).

Within the polar zone, the correlation between the intensity of herbivory combined with carnivory and latitude was most negative (Figure 5; $z_r = -0.34$, CI_{95} from -0.46 to -0.23 , $n = 79$) and robust against non-significant studies (fail-safe number equals $10.4n$). This correlation was fourfold greater ($Q_B = 14.6$, $df = 1$, $p = 0.0001$) than the correlation observed at lower latitudes ($z_r = -0.09$,

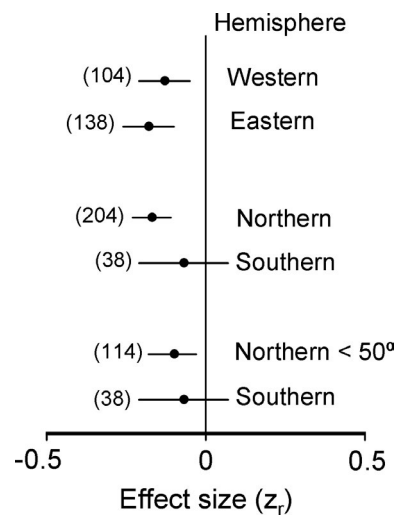


FIGURE 4 The strength of latitudinal changes in the intensity of herbivory and carnivory (combined) in different hemispheres. For explanations, refer to Figure 1; for statistical analysis, see text

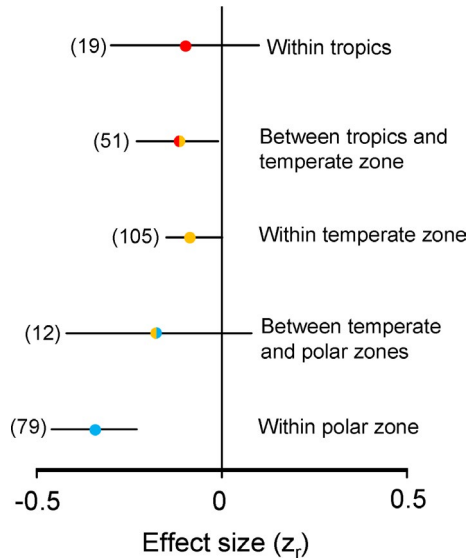


FIGURE 5 The strength of latitudinal changes in the intensity of herbivory and carnivory (combined) within and between different climate zones. For explanations, refer to Figure 1; for statistical analysis, see text

increase in the latitudinal midpoints of studied gradients ($Q = 12.2$, $df = 233$, $p = 0.0005$). However, this pattern emerged only due to herbivory and carnivory by ectothermic animals (Figure 6a; $Q = 7.71$, $df = 191$, $p = 0.0055$) and was not statistically significant for endotherms (Figure 6b; $Q = 0.63$, $df = 31$, $p = 0.43$). The correlation between parasitism and latitude did not change with latitude ($Q = 0.06$, $df = 33$, $p = 0.81$).

Variation associated with methodology

Studies based on original data and studies combining published data yielded similar ES ($Q_B = 2.34$, $df = 1$, $p = 0.13$). The strength of latitudinal changes did not depend on the extension of the gradient (herbivory: $Q = 2.78$, $df = 216$, $p = 0.10$; carnivory: $Q = 0.57$, $df = 43$, $p = 0.45$; parasitism: $Q = 0.80$, $df = 33$, $p = 0.91$). Studies that estimated community-wide herbivory and studies that estimated herbivory on individual plant species yielded similar ES ($Q_B = 0.27$, $df = 1$, $p = 0.60$). Studies that used standardised prey (artificial bird nests or in-

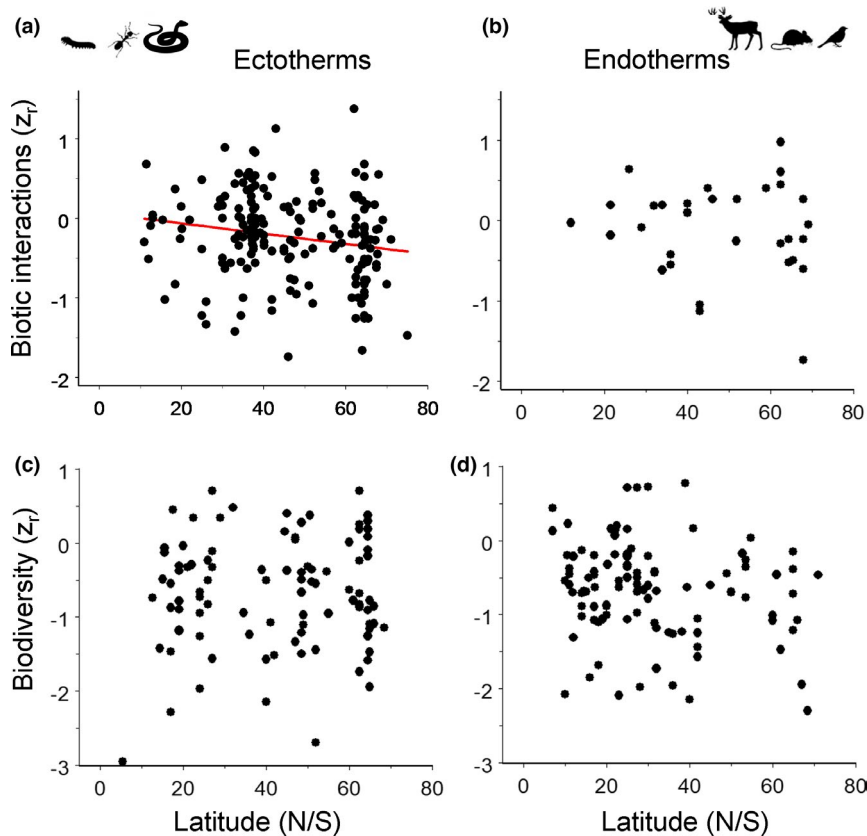


FIGURE 6 Latitudinal changes in the strength of the correlation with latitude for herbivory and carnivory (a, b) and for the biodiversity of herbivores, carnivores and omnivores (c, d) for ectothermic (a, c) and endothermic (b, d) animals

CI_{95} from -0.15 to -0.03 , $n = 175$). Consistently, the correlation between intensity of biotic interactions and latitude decreased (i.e. became more negative) with an

sect prey models, standard seeds or the same non-local plant genotypes) yielded twofold stronger negative correlations with latitude than did studies that used natural

local prey, but only when the consumers (herbivores and carnivores combined) were ectothermic (Figure 7; $Q_B = 4.44$, $df = 1$, $p = 0.035$). When the carnivores were endothermic, studies using standardised and natural prey yielded similar (non-significant) correlations (Figure 7; $Q_B = 0.003$, $df = 1$, $p = 0.96$).

Publication and confirmation biases

We found an increase in the standardised ES with an increase in sample size (the number of study sites) in studies addressing herbivory and carnivory ($\tau = 0.088$, $p = 0.03$). We found this evidence for publication bias only among studies that aimed at testing the LBIH ($\tau = 0.13$, $p = 0.007$) but not among other studies ($\tau = 0.04$, $p = 0.61$). Studies addressing parasitism did not suffer from publication bias ($\tau = -0.16$, $p = 0.14$). We did not find association between ES and journal IF (herbivory and carnivory: $Q = 0.13$, $n = 277$, $p = 0.72$; parasitism: $Q = 0.05$, $n = 40$, $p = 0.82$) or publication year (herbivory and carnivory: $Q = 0.67$, $n = 277$, $p = 0.41$; parasitism: $Q = 0.05$, $n = 40$, $p = 0.82$).

Only studies that tested the LBIH found support for it ($z_r = -0.15$, CI_{95} from -0.20 to -0.09 , $n = 209$), whereas other studies (both non-hypothesis-driven or testing other hypotheses) yielded no latitudinal changes ($z_r = -0.01$, CI_{95} from -0.11 to 0.09 , $n = 108$); the difference between these two groups of studies was significant ($Q_B = 5.50$, $df = 1$, $p = 0.02$).

Comparison between gradients in biotic interactions and biodiversity

The latitudinal decrease in intensity of herbivory and carnivory ($z_r = -0.17$) was fourfold weaker ($Q_B = 61.0$,

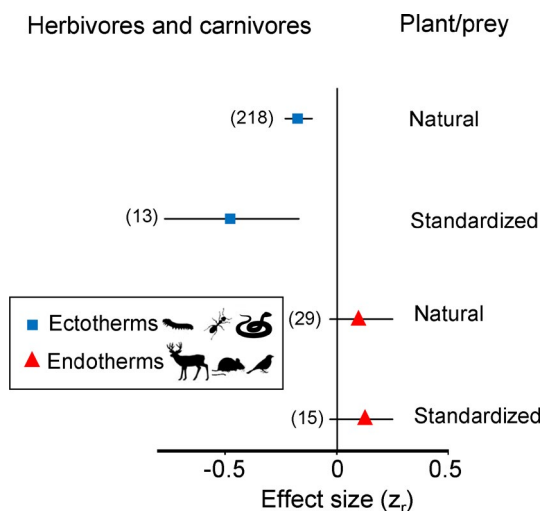


FIGURE 7 The strength of latitudinal changes in pressure by ectothermic and endothermic carnivores on standardised and natural prey. For explanations, refer to Figure 1; for statistical analysis, see text

$df = 1$, $p < 0.0001$) than the latitudinal decrease in the diversity of taxonomic groups consisting of herbivores, carnivores and/or omnivores ($z_r = -0.63$; Table SM3 in Zvereva & Kozlov, 2021b). Furthermore, the difference in latitudinal patterns between ectothermic and endothermic animals was found in biotic interactions (Figure 3) but not in diversity ($Q_B = 0.02$, $df = 1$, $p = 0.90$). Similarly, a poleward increase in the strength of latitudinal correlations was found in biotic interactions (Figure 5) but not in diversity ($Q_B = 1.81$, $df = 4$, $p = 0.77$). The correlation between biotic interactions and latitude became more negative with an increase in the latitudinal midpoint of each gradient for herbivory combined with carnivory ($Q = 12.5$, $df = 233$, $p = 0.0004$) mostly due to interactions involving ectothermic animals (Figure 6a). By contrast, the correlation between biodiversity and latitude did not show latitudinal changes either for all animals combined ($Q = 0.26$, $df = 198$, $p = 0.61$) or for ectothermic and endothermic animals analysed separately (Figure 6c,d; ectotherms: $Q = 0.11$, $df = 95$, $p = 0.74$; endotherms: $Q = 0.46$, $df = 101$, $p = 0.49$). Publication bias was found in studies testing the LBIH but not in studies addressing the latitudinal diversity gradient ($\tau = 0.015$, $p = 0.76$).

DISCUSSION

The latitudinal pattern in biotic interactions

Our meta-analysis has demonstrated a significant, although small (sensu Cohen, 1988), poleward decrease in the intensity of the explored biotic interactions. Nevertheless, this pattern is not ubiquitous, as the strength and even the sign of latitudinal changes in biotic interactions vary among organisms involved in the interactions and among environments. Furthermore, the detected patterns in some cases are not robust and are influenced by several biases. Consequently, only some of our hypotheses concerning the sources of variation in the LBIH have been supported by our meta-analysis of herbivory, carnivory and parasitism (Table 1). Below, we discuss the sources of variation in latitudinal patterns which allowed detection of the conditions where the LBIH is applicable and identification of the scope of this hypothesis for trophic interactions in terrestrial ecosystems.

Variation associated with the organisms involved

The greatest variation in latitudinal patterns is associated with the feeding strategies of the consumers involved in biotic interactions. We found that the intensities of both herbivory and carnivory generally exhibit similar latitudinal patterns that fit the LBIH, as they decreased from low to high latitudes. Similarity in correlation with

TABLE 1 The overview of main hypotheses about general pattern and sources of variation in latitudinal gradient in biotic interactions and the results of their testing

Hypothesis	Supported	Illustrated	Comment
The intensity of biotic interactions decreases from the equator to the poles	Yes	Figure 1	Interpreted as the overall support for LBIH
This decrease is similarly expressed across studied trophic interactions	No	Figure 1	Herbivory and carnivory decrease, whereas parasitism increases towards the poles
Latitudinal changes in the intensity of biotic interactions depend on the thermoregulation strategy of the involved organisms	Yes	Figure 3	Latitudinal changes are significant for ectothermic consumers only
Strength of latitudinal gradient in biotic interactions differs between climate zones	Yes	Figure 5	The latitudinal gradient is strongest at high latitudes
Latitudinal changes in the intensity of biotic interactions are strongest between tropical and temperate zones	No	Figure 5	These changes are not robust and do not differ from changes within tropical and temperate zones
Strength of latitudinal gradient in biotic interactions differs between Northern versus Southern and Eastern versus Western hemispheres	No	Figure 4	Slight difference between Northern and Southern hemispheres disappears when high latitude data (present in Northern hemisphere only) are excluded
Latitudinal changes in herbivory/carnivory on standardised plant/prey are stronger than on local plant/prey due to their pre-existing anti-predator adaptations	Yes	Figure 7	Valid for ectothermic carnivores only
The publication bias favours small-sample studies supporting LBIH	Yes	Text	Valid only for studies aimed at testing the LBIH
Latitudinal changes in biotic interactions and in biodiversity follow similar patterns in terms of both magnitude of the effect and sources of variation	No	Figure 6, text	These two gradients differ fourfold in strength and do not share many sources of variation

Abbreviation: LBIH, latitudinal biotic interaction hypothesis.

latitude between herbivory and carnivory may indicate that their intensities are shaped by the same factors. By contrast, parasitism shows the opposite pattern, that is an increase with the increasing latitude. The lack of a decrease in the parasitism rate at high latitudes may be explained by the fact that parasites live within or on their host bodies, where they obtain full or partial protection from unfavourable environmental conditions (Hawkins, 1994). This may be especially true for endoparasites (Péré et al., 2013), which comprise 92% of the data on parasitism in our database.

The contrasting latitudinal changes in carnivory and parasitism were discovered earlier for herbivorous insect prey in a single boreal forest gradient (Zvereva et al., 2020b) and in several between-site comparisons (Cornelissen & Stiling, 2009; Hawkins et al., 1997; Libra et al., 2019). Within the individual study systems, the reciprocal patterns observed between carnivory and parasitism may result from the increase in parasitoid mortality with an increase in carnivory on the parasitised hosts (Libra et al., 2019) and/or from parasite preference for hosts that experience lower risk of predation (Murphy et al., 2014). By summarising the outcomes of multiple independent studies on various groups of parasites, including insect parasitoids, blood parasites and other parasites of vertebrate animals, our meta-analysis revealed the fundamental nature of the

differences in latitudinal patterns between carnivory and parasitism.

Another important source of variation was identified when we compared the interactions involving consumers with different thermoregulation strategies. Both herbivory and carnivory by ectothermic animals (represented by invertebrates and reptiles in our study) significantly decreased with an increase in latitude. By contrast, the biotic interactions involving endothermic animals (mammals and birds) did not change with latitude. Importantly, the latitudinal patterns differed significantly between ecto- and endothermic carnivores (Figure 3), whereas the differences between ecto- and endothermic herbivores did not reach statistical significance.

The latitudinal changes in the intensity of herbivory and carnivory were found in ectothermic animals only, presumably because their body temperature tends to follow the environmental temperatures, thereby rendering them particularly sensitive to their environment (Huey et al., 2012). Our result is in line with the conclusion (Buckley et al., 2012) that the different energetic and performance implications of body temperature regulation for ectotherms and endotherms are central to understanding their broad-scale ecological patterns, which typically span substantial gradients in temperature and other environmental variables. Nevertheless, ectothermic and endothermic animals differ in many other traits

(Buckley et al., 2012), and therefore, their differences in latitudinal changes of biotic interactions may reflect not only their thermoregulation strategy but also other aspects of their interactions with the abiotic environment.

Geographic variation

The LBIH was originally developed based on comparisons between tropical and temperate zones (Coley & Kursar, 2014; Dobzhansky, 1950; Fischer, 1960; Schemske et al., 2009). In our study, the intensity of biotic interactions was significant for comparisons between these zones (Figure 5). However, the strength of gradients located entirely within the tropical and temperate zones was similar to the strength of the gradients crossing the border between these zones. These results indicate that changes in the intensity of biotic interactions are continuous through tropical and temperate zones. At the same time, contrary to expectations, the strength of the latitudinal gradients significantly (and robustly) increased at latitudes above 50–60° (depending on continents), and the global latitudinal pattern in the intensity of biotic interactions emerged mostly due to studies conducted in subpolar and polar regions.

The hypothesis that the latitudinal gradient in herbivory becomes stronger at high latitudes was raised by Kozlov et al. (2013). However, testing for this hypothesis appeared possible only recently, following the accumulation of sufficient data from polar regions. We also increased the number of ESs from high latitudes by dividing data from several global studies (Hargreaves et al., 2019; Kozlov et al., 2015; Peco et al., 2014; Zhang et al., 2016) into climate zones and calculating the correlations within these zones. Consequently, the presentation of the polar zone in our database (26.2% of studies) approximately corresponds to the proportion of the terrestrial area of this zone on Earth (23%; Romanova et al., 2015). The strong gradient in the intensity of biotic interactions at high latitudes stresses the importance of adequate representation of polar regions in macroecological research addressing global patterns in biota. The urgent need for data collection from these regions is justified by disproportionately rapid contemporary climatic change (Walther et al., 2002) which has already disrupted some historical gradients in biotic interactions, for example bird nest predation (Kubelka et al., 2018).

The importance of temperature as a primary driver of latitudinal gradients in biotic interactions, demonstrated in a number of studies (Kozlov et al., 2015; Peco et al., 2014; Romero et al., 2018), is indirectly supported by the absence of a latitudinal decrease in herbivory and carnivory involving endothermic animals. To test the hypothesis that the stronger correlation between biotic interactions and latitude in the polar zone relative to the temperate and tropical zones is explained by a non-linear poleward decrease in temperature, we calculated

the rate of the latitudinal change in mean annual temperatures, derived from records collected over 84 years from 7706 weather stations (Figure 1e in Wang & Dillon, 2014). This rate was found to differ considerably between climate zones, from 0.05°C per one degree of latitude in the tropical zone to –0.60°C in the temperate zone and then to –1.57°C in the polar zone. Thus, as indicated by Terborgh (1973), the environmental harshness increases poleward more rapidly at high latitudes than at temperate latitudes. We suggest that this difference is one likely reason behind the variation in the strength of the latitudinal gradient in biotic interactions for ectothermic organisms among the climate zones.

The strong association between the intensity of biotic interactions and latitude in the polar region may be driven by an increasingly sharp poleward decrease in the temperatures that are suitable for the activity of animals, and this decrease then constrains ectotherms much more than endotherms (Buckley et al., 2012). The ectothermic animals at high latitudes live in climates that are cooler than the animals' physiological optima (Deutsch et al., 2008). Therefore, despite the greater temperature tolerance of high-latitude organisms relative to low-latitude organisms (Sunday et al., 2011), even a small latitudinal decrease in temperature in polar regions may cause strong declines in the performance and activity of ectotherms.

Variation in methodology

Our meta-analysis did not confirm the expected impacts of a number of methodological issues, such as the span of the gradient or the difference between a gradient lying within one climatic zone compared with two or three zones, on the variation among studies (Table 1). We also did not find support for the suggestion (Anstett et al., 2016) that different patterns emerge from studies measuring herbivory at the community level and from studies conducted with individual plant species. We are aware of the single study that found a significant difference between latitudinal patterns in community-wide herbivory and herbivory on individual plant species (Zvereva et al., 2020a). Our meta-analysis did not confirm the generality of these differences; however, this could be due to insufficient number of latitudinal studies based on community-wide estimates of interaction intensity (6% of herbivory data in our database).

The important methodological source of variation in latitudinal patterns revealed by our meta-analysis is the type of plant/prey which had been exposed at different latitudes to estimate herbivore/carnivore pressure. We found that herbivory and carnivory measured on standardised prey, including non-native plant species/genotypes (Lu et al., 2019) or their seeds (Chen et al., 2017; Hargreaves et al., 2019), plasticine insect models (Roslin et al., 2017; Zvereva et al., 2019), non-native

live insect prey (Jeanne, 1979) and artificial bird nests (McKinnon et al., 2010), yield stronger latitudinal patterns than are obtained when predation is measured on natural prey, at least for ectothermic consumers. This difference can be explained by the latitudinal changes in local adaptations of native plant/prey, for example in anti-herbivore defences in plant seeds (Chen et al., 2017; Moreira et al., 2020) and in the behavioural and life history anti-predator adaptations in birds (Díaz et al., 2013; Freeman et al., 2020), whereas standardised models did not participate in evolution (Freeman et al., 2020).

Our meta-analysis indicates that local anti-herbivore and anti-predator adaptations considerably modify the latitudinal gradient in herbivory and predation. In particular, adaptations that have evolved in response to high predation pressure may counter-balance the effects of predation driven by climate and thereby dampen the geographic patterns in interaction rates (Freeman et al., 2020). Overall, the use of standard plant/prey leads to an overestimation of the strength of latitudinal gradients in biotic interactions actually existing in natural populations, at least for ectothermic consumers.

However, the assessment of predation measured using standardised plants/prey (e.g. Hargreaves et al., 2019; McKinnon et al., 2010; Roslin et al., 2017) is of utmost importance for the understanding of macroecological patterns and processes, because this method avoids the impact of variations in plant/prey across multiple localities on the outcomes of latitudinal studies. Nevertheless, it remains unclear, whether these data are suitable for predicting the effects of projected climate changes on predation pressure by extrapolation of spatial (i.e. latitudinal) patterns to temporal (i.e. climate change) patterns, as it was made by Romero et al. (2018) based on attack rates on plasticine caterpillar models (Roslin et al., 2017) or by Orrock et al. (2015) based on predation on standardised seeds. To justify these extrapolations, we need more information on whether adapted populations of both the predator and prey will migrate to new habitats following climate change or whether local populations will evolve adaptations to their new environmental conditions. The answer may also depend on the nature of the adaptations: many morphological or chemical adaptations that evolve over a long time are unlikely to follow relatively fast changes occurring in Anthropocene, but other adaptations (e.g. behavioural ones) can evolve quite rapidly.

Biases in latitudinal studies of biotic interactions

Our conclusions about the overall significance of the latitudinal gradient in biotic interactions may be influenced by an uneven presentation of latitudinal studies among different groups of animals. Our database is dominated

by studies of herbivory and carnivory imposed by ectothermic animals (66.2% of all data; 89.9% of herbivory data), which showed the strongest decrease with the increase in latitude compared with endotherms and parasitoids. Further bias in this direction was imposed by our decision to exclude data on interactions that have been influenced by human activities, which (as mentioned above) have particularly affected latitudinal studies on mammalian herbivory. However, this overrepresentation of interactions involving ectotherms in our database is in line with their greater importance relative to endothermic animals in terrestrial ecosystems (Bar-On et al., 2018). Similarly, the overrepresentation of studies conducted within the temperate zone corresponds to the proportion of this zone on Earth (47%: Romanova et al., 2015). Thus, our database is not likely to suffer from either object selection bias or geographic bias.

The analysis of our database demonstrated the existence of publication bias that favours studies supporting the LBIH. This could be due to a decision by a researcher to submit the results, the ranking by reviewers or the final decision of the editors (Jennions et al., 2013). For example, Moles (2013) revealed citation bias in studies testing the LBIH by demonstrating that papers supporting the traditional idea are cited six times more often than papers that do not support it. This bias presumably prompts the authors to preferentially publish confirmatory results because they have a higher potential to be cited. Notably, we found publication bias only for studies that directly tested the LBIH. Publication bias can considerably influence the results of consequent meta-analyses (Jennions et al., 2013), thus leading to canonisation of false ideas (Nissen et al., 2016).

Our results also hint at the existence of confirmation bias—the unconscious tendency of researchers to find support for their hypotheses and expectations, which generally leads to an overestimation of the effects under study (Holman et al., 2015; Zvereva & Kozlov, 2019). In our meta-analysis, the proportion of hypothesis-driven studies (66%) was much greater than in the ecological and evolutionary research in general (26%: Betts et al., 2021), and studies that aimed at testing the LBIH found considerably stronger effects of latitude on the intensity of biotic interactions than did studies testing other hypotheses. This result suggests that formulating the hypothesis in the study increases the probability of finding support for it as it is typical for confirmation bias (Zvereva & Kozlov, 2019). The alternative explanation is that the hypothesis was included into a publication only if the results supported it. The latter phenomenon is known as HARKing—Hypothesising After the Results are Known (Kerr, 1998). By contrast, non-hypothesis-driven studies (sometimes undervalued by the academic community), as well as studies testing hypotheses other than the LBIH, are likely to yield unbiased results because this research escapes both the confirmation bias that pervasively influences hypothesis testing (Loehle,

1987) and publication bias, as discussed above. Thus, despite the immense value of hypothesis-driven science, non-hypothesis-driven research remains crucial for obtaining adequate information about our world (Betts et al., 2021; Tripathi et al., 2018).

Confirmation bias is difficult to overcome due to its unconscious nature (Zvereva & Kozlov, 2021a), and this bias will likely lead to an overestimation of the strength of latitudinal changes in biotic interactions as long as LBIH is accepted by the majority of scientists. However, the reviewed research field yet shows no sign of any loss of LBIH popularity in the scientific community. In spite of an accumulation of disconfirming evidence and the publication of several reviews that strongly oppose the LBIH (Moles, 2013; Moles et al., 2011; Moles & Ollerton, 2016; Poore et al., 2012), we did not find any temporal shift in the reported strength of latitudinal changes in biotic interactions. This indicates that the influence of the LBIH is still high and that all the biases listed above remain in full force, potentially leading to overestimation of the gradient strength in meta-analysis. Nevertheless, the biases discussed above, although potentially affecting the magnitude and significance of the overall effect of latitude on biotic interactions, do not question the existence of the identified sources of variation in outcomes of latitudinal studies.

Gradients in biotic interactions versus biodiversity

The overall strength of the latitudinal gradient in our set of diversity data ($z_r = -0.63$) is very similar to the estimates presented by Hillebrand (2004) and Kinlock et al. (2018), based on their entire data sets that included all groups of organisms ($z_r = -0.67$ and $z_r = -0.48$, respectively). This similarity indicates that the latitudinal trend in the diversity of the selected groups of animals (herbivores, carnivores and omnivores), which comprised 16% and 21% of all the data used in previously published meta-analyses (Hillebrand, 2004; Kinlock et al., 2018), is representative of all organisms in a variety of ecosystems.

The intensities of both herbivory and carnivory and the diversity of organisms involved in these interactions showed a significant decrease from low to high latitudes. However, the gradient in biodiversity was fourfold stronger than the gradient in biotic interactions, indicating that either these two gradients are shaped by different factors or these two response variables have different sensitivity to latitudinal changes in the same factor.

We also revealed considerable differences in the sources of variation between gradients in the biotic interactions explored in our meta-analysis and in the biodiversity explored by Hillebrand (2004) and Kinlock et al. (2018). For example, Hillebrand (2004) found an increase in the strength of the diversity gradient with increasing trophic level, with a nearly twofold difference between

herbivores and carnivores, whereas we found a similar gradient strength for herbivory and carnivory (Figure 1). In the meta-analysis by Kinlock et al. (2018), mammals showed the strongest latitudinal gradient in diversity ($z_r = -0.70$), while mammalian herbivory and mammalian carnivory did not change with latitude ($z_r = 0.004$). Both of these previously published meta-analyses (Hillebrand, 2004; Kinlock et al., 2018) found considerable differences in the strength of the biodiversity gradient among continents, whereas the latitudinal gradients in biotic interactions were similar in all continents.

Importantly, neither Hillebrand (2004) nor Kinlock et al. (2018) found differences in the strength of the diversity gradient between endothermic and ectothermic animals. We confirmed this conclusion for our subset of the diversity data, whereas endotherms and ectotherms showed different latitudinal patterns in biotic interactions. The strength of the correlation between the intensity of the biotic interactions and latitude increased with latitude for ectothermic animals, reaching its maximum in the polar zone (Figures 5 and 6). By contrast, the strength of the biodiversity gradient did not show any latitudinal changes (Figure 6). These two contrasts hint at greater importance of temperature in shaping the latitudinal gradient in the intensity of biotic interactions relative to the biodiversity gradient. Great differences in the sources of variation between the gradients in biotic interactions and diversity lead us to conclude that global gradients in biodiversity and in biotic interactions are most probably shaped by different factors.

CONCLUSIONS

Our meta-analysis demonstrated a significant poleward decrease in the intensity of herbivory and carnivory, thus supporting the LBIH for these interactions. However, the overall strength and significance of this latitudinal gradient are likely overestimated due to publication and confirmation biases. Our analysis of the sources of variation in the outcomes of latitudinal studies allowed us to identify conditions where this hypothesis is applicable and thus clarify the scope of the LBIH within trophic interactions in terrestrial ecosystems. The LBIH finds unequivocal support at high latitudes, for ectothermic herbivores and carnivores and when their host plant/prey are standardised (i.e. they lack local anti-predator adaptations) (Table 1). The most significant variation in outcomes of studies exploring latitudinal changes in biotic interactions is associated with temperature, indicating the importance of latitudinal climate gradients as a major driver of the latitudinal pattern in biotic interactions, presumably through changes in the activity of the involved organisms. In addition, the considerable differences observed in herbivory and carnivory on natural versus standardised plant/prey hint at the importance of variation in local anti-herbivore and anti-predator

adaptations in shaping latitudinal gradients in biotic interactions by dampening the underlying geographic pattern. The significant differences in the magnitude and the dissimilarities in the sources of variation between latitudinal gradients in biotic interactions and in biodiversity suggest that these two macroecological patterns are likely driven by different factors and are only tenuously associated with each other.

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AUTHOR CONTRIBUTIONS

ELZ and MVK formulated goals and designed methodology, ELZ extracted data for meta-analysis, conducted meta-analysis and wrote the first draft of the manuscript, MVK participated in the writing of later drafts.

DATA AVAILABILITY STATEMENT

The data sets used for the analyses are archived in Dryad Digital Repository (<https://doi.org/10.5061/dryad.z8w9ghxcd>).

ORCID

Elena L. Zvereva  <https://orcid.org/0000-0003-2934-3421>

Mikhail V. Kozlov  <https://orcid.org/0000-0002-9500-4244>

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