Predation and parasitism on herbivorous insects change in opposite directions in latitudinal gradient crossing boreal forest zone

Elena L. Zvereva [1], Vitali Zverev [1], Mikhail V. Kozlov [1]

[1] Department of Biology, University of Turku, 20014 Turku, Finland

Correspondence: Elena L. Zvereva. E-mail: elezve@utu.fi, Tel. +358503427587

Running title: Predation and parasitism change with latitude

Abstract

1. The Latitudinal Biotic Interaction Hypothesis (LBIH) predicts that the strength of various biotic interactions decreases from low to high latitudes. Inconsistency between studies testing this hypothesis may result from variations among different types of interactions and among study systems. Therefore, exploration of multiple interactions within one system is required to disentangle latitudinal patterns across individual interactions and to evaluate latitudinal changes in the overall impact of enemies on prey.
2. We tested the prediction based on the LBIH that the pressure of natural enemies on herbivorous insects decreases with increase in latitude across the boreal forest zone. We also asked whether the impacts of major groups of these enemies exhibit similar latitudinal patterns and whether these patterns are consistent across study years.
3. In 10 forest sites located from 60°N to 69°N in Northern Europe, each summer, from 2016–2019, we measured (i) mortality of three groups of leafmining insects caused by birds, ants, parasitoids and unknown factors, ii) bird attacks on caterpillar-shaped plasticine models, and iii) birch foliar damage caused by defoliators and leafminers.
4. Latitudinal patterns in both insect herbivory on birch and top-down pressure on herbivorous insects varied considerably and inconsistently among the four study years, so that only some of the year-specific correlations with latitude were statistically significant. Nevertheless, meta-analysis combining correlations across years, preys and enemies revealed general decreases in predation by birds (on both natural and model prey) and ants, but an increase in parasitism rates, from low to high latitudes.
5. We revealed that the direction of latitudinal changes in the strength of biotic interactions is interaction-specific: predation and herbivory support LBIH, whereas parasitism exhibits an opposite trend. Consequently, the overall impact of natural enemies on herbivorous insects did not change with latitude and was therefore an unlikely reason for the poleward

decrease in herbivory observed in our gradient. Considerable among-year variation in the strength of the latitudinal patterns in all the studied interactions suggests that this variation is a widespread phenomenon.

Keywords: Ant predation, bird predation, boreal forests, insect herbivory, leafminers, plasticine prey models, latitudinal biotic interaction hypothesis, latitudinal gradient, parasitism, top-down factors

1 INTRODUCTION

The long-standing Latitudinal Biotic Interaction Hypothesis (LBIH, hereafter) predicts that the strength of various biotic interactions is highest in tropical areas and decreases from low to high latitudes (Schemske et al. 2009). This hypothesis has a long history, and a number of reasons for the increase in the intensity of biotic interactions towards equator have been suggested, including a ‘benign’ climate and an increased diversity and abundance of organisms (Wallace 1878; Dobzhansky 1950; MacArthur 1972; Schemske et al. 2009). Most frequently, the LBIH has been associated with a latitudinal diversity gradient—the most impressive biogeographic pattern on Earth (Schemske et al. 2009). Exploration of geographical variations in species interactions provides invaluable information about the factors affecting the structure and functioning of ecosystems (Travis 1996) and advances our understanding of such fundamental processes as co-evolution, natural selection, adaptation and speciation (Schemske et al. 2009; Anstett et al. 2018).

The LBIH was originally developed based on the striking difference in biodiversity and in the intensity of biotic interactions between tropical and temperate biomes (Dobzhansky 1950; MacArthur 1972). Later on, the LBIH was tested at different scales—from global patterns across biomes to within-biome gradients. These studies provided mixed support for the LBIH (Adams & Zhang 2009; Moles et al. 2011a; Kozlov et al. 2015a; Roslin et al. 2017; Baskett & Schemske 2018), and the variability of outcomes between case studies inspired the search for the sources of controversy surrounding latitudinal patterns in biotic interactions (Anstett et al. 2016). One of these sources may be the variation between different types of interactions.

The LBIH was especially frequently tested by exploring insect herbivore pressure on plants, and these studies include many plant–herbivore systems (Moles et al. 2011a; Kozlov et al. 2015a; Moreira et al. 2015). Multiple factors have been suggested to explain latitudinal patterns in herbivory, in particular the changes in plant anti-herbivore defences (Anstett et al. 2018; Moreira et al. 2018). However, many studies either did not find latitudinal changes in plant defences, or failed to demonstrate a link between changes in plant defences and herbivory (Moles et al. 2011b). Therefore, natural enemies have been suggested as a factor driving latitudinal patterns in insect herbivory (Bjorkman et al. 2011). However, latitudinal studies of predator–prey interactions focused mostly on seed predation (Moles & Westoby 2003; Peco et al. 2014; Hargreaves et al. 2019) and bird nest predation (McKinnon et al. 2010; Kubelka et al. 2018). Only a few studies tested the LBIH with data on the natural enemy impact on herbivores, and these studies demonstrated specific responses of different groups of enemies. For example, while predation intensity by arthropods on invertebrates generally decreased with an increase in latitude (Jeanne 1979; Roslin et al. 2017; Zvereva et al. 2019), bird predation showed no clear latitudinal pattern (Lövei & Ferrante 2017; Roslin et al. 2017) or it even increased from low to high latitudes (Zvereva et al. 2019). Similarly, latitudinal patterns in predation on seeds differ between vertebrate and invertebrate predators (Peco et al. 2014; Hargreaves et al. 2019). The parasitism on herbivorous insects usually does not show latitudinal changes (Hawkins et al. 1997; Stireman et al. 2005; Moreira et al. 2015), but it sometimes increases with an increase in latitude (Rull et al. 2009).

Thus, the impacts of different enemies on the same prey may exhibit different latitudinal changes. Consequently, revealing the latitudinal pattern in the overall enemy pressure on herbivorous insects requires the simultaneous measurements of mortality caused by all groups of predators and parasitoids. This approach is difficult to implement within one study system, but leafminers (i.e. herbivorous insects that feed within a plant leaf) provide a unique opportunity to realise this approach. The fate of each leafmining larva can be traced, and the sources of larval mortality, such as ants, birds and parasitoids, can be identified by investigating the leaf mines (Zvereva & Kozlov 2006; Cornelissen & Stiling 2009; Low et al. 2009). Therefore, leafminers allow simultaneous assessment of the impacts of multiple top-down factors on live natural prey, thereby offering a unique opportunity to study latitudinal patterns in trophic interactions.

The inconsistent outcomes of studies testing the LBIH may also reflect the variation in the methods used to measure the intensity of trophic interactions (Anstett et al. 2016; Roslin et al. 2017). The majority of latitudinal studies of predation on invertebrates have been conducted using plasticine caterpillar models (Lövei & Ferrante 2017; Roslin et al. 2017; Zvereva et al. 2019; but see Jeanne 1979). However, these artificial prey lack many characteristics of natural prey, such as odour and movement, so that estimates of predation rates obtained from prey models do not reflect the real values of predation pressure on herbivorous insects (Lövei & Ferrante 2017). In addition, the artificial prey method may produce biased results due to the physical characteristics of plasticine (discussed by Muchula et al. 2019; Zvereva et al. 2019). The visibility of attack marks, and especially of the weak marks left by invertebrate predators, decreases considerably with decreases in ambient temperature (Muchula et al. 2019), leading to an underestimation of predation rates at high latitudes. At the same time, the use of standardized prey (live insect larvae: Jeanne 1979; plasticine caterpillars: Roslin et al. 2017; artificial bird nests: McKinnon et al. 2010; seeds: Hargreaves et al. 2019) may have better potential for detecting latitudinal patterns in predation intensity, because natural prey may exhibit latitudinal changes in anti-predator adaptations (Toju & Sota 2006; Chen et al. 2017). The simultaneous use of natural and standardised prey would therefore contribute to better understanding of advantages and disadvantages of these two approaches to study latitudinal patterns in the strength of biotic interactions.

In the present study, we used leafmining insects feeding on three host plants (two birch species, *Betula pendula* and *B. pubescens*, and rowan, *Sorbus aucuparia*), in conjunction with plasticine models for the assessment of bird predation, to test the prediction of the LBIH that the pressure of natural enemies on herbivorous insects decreases with increase in latitude, and to explore variations in latitudinal patterns among different groups of natural enemies and among four study years. We asked the following questions: (i) whether the impacts of major groups of natural enemies (predators, including birds and ants, and parasitoids) on herbivorous insects decrease from low to high latitudes; (ii) whether these latitudinal changes are consistent among the groups of natural enemies and across four study years; and (iii) whether latitudinal changes in herbivory are associated with latitudinal changes in predation and parasitism. We answered these questions using the data collected from a 1000 km long environmental gradient in boreal forests of Northern Europe. This gradient has already been used in several latitudinal studies (Kozlov 2008; Kozlov et al. 2013; Zverev et al. 2017; Finér et al. 2019; Zvereva et al. 2020), so it allows comparisons of patterns observed in different groups of biota.

2 MATERIALS AND METHODS

2.1 Study region and study sites

The study was performed in ten sites that form environmental gradient, which extends across the entire boreal (taiga) forest zone, from the northern limit of broadleaved forests to the northern tree line. The sites were selected in unevenly aged, unmanaged old-growth forests of a similar type located from 60°N near St. Petersburg to 69°N close to Murmansk in NW Russia (sites R60–R69: Fig. S1, Table S1). The mean annual temperature (MAT) within this gradient (estimated using New_LocClim: FAO, 2006) decreases from +4.28°C in the southernmost site to -0.94°C in the northernmost site, and the mean annual precipitation (MAP) varies from 434 to 606 mm (Table S1). The regional tree species pool consisted of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), downy birch (*B. pubescens*), silver birch (*B. pendula*), European aspen (*Populus tremula*), rowan (*S. aucuparia*) and goat willow (*Salix caprea*). The field layer vegetation was dominated by dwarf shrubs, with bilberry (*Vaccinium myrtillus*) contributing, on average, 63% to the total field layer cover. For more details, consult Zvereva et al. (2020).

2.2 Assessment of leafminer mortality

We collected birch leaves mined by the larvae of *Eriocrania* spp. (Fig. 1a; between 10 and 29 June) and *Stigmella* spp. (Fig. 1b; between 8 and 29 August), and rowan leaves mined by the larvae of several moth species (Fig. 1c; between 8 and 29 August); sampling was conducted at each of our study sites annually from 2016–2019. The last instar larvae of *Eriocrania* spp. reach 10 mm in length and form a blotch mine 300–600 mm^2 in size, whereas the larvae of *Stigmella* spp. reach 5 mm in length and form a gallery or gallery-blotch mine 30–120 mm^2 in size, depending on the species. The same experienced persons (V.Z. and M.V.K.) jointly searched for the mined leaves at all sites and during all study years. We attempted to obtain 20–50 mines of each of three groups of moths from each study site annually. All discovered mines had been collected; the smallest sampled mines had an area of 2–3 mm^2. In total, we analysed 6216 mines of 12 moth species (Tables S1–S4).

The samples were sorted by leafminer species (using an online identification guide: Ellis 2016) and then classified as either empty mines left by larvae which had successfully completed their development (i.e. survived individuals) or mines containing dead larvae or mines that had been opened by predators (Fig. S2). The mines containing dead larvae were classified as killed by parasitoids if a parasitoid larva or pupa was found inside the undamaged mine (Fig. S2e). If no signs of parasitism were discovered, then the death was attributed to unknown reasons(Fig. S2d). All larvae that failed to reach 10% of their final size were classified as having died from unknown reasons because they were too small (Fig. S2i) to have been a target for predators or parasitoids. If the mine contained no dead larva and only a small part of a single epidermal wall of the mine was damaged (usually in the form of one or more small round holes: Fig. S2c), then the larva was classified as having been eaten by ants. If both walls of the mine were punched through and severely damaged (Fig. S2f, g), the mortality was attributed to birds (Zvereva & Kozlov 2006; Kozlov et al. 2017). We are not aware of any other groups of predators that significantly contribute to the mortality of leafminers in our study region. All mines were inspected by M.V.K.

2.3 Assessment of bird attack rates on artificial prey

We fabricated our prey models from non-toxic, unscented, soft modelling clay (Chemical plant ‘Luch’, Yaroslavl, Russia) of green and brown colours to imitate the natural colours of palatable caterpillars. Green wire 0.3 mm in diameter was used to attach two plasticine models (28–32 mm length and 3.5–4 mm diameter) of different colours to thin branches of each of five haphazardly selected mature (>3 m height) birches (Fig. 1d) at a height of 1.2–1.8 m and at least 50 cm apart. The models were exposed from 10–12 June and checked on 26–30 June, 8–12 August and 23–29 August in 2016–2019. During each inspection, we counted plasticine caterpillars with beak marks left by birds (Fig. 1d; the marks were identified according to Low et al. 2014) and then remoulded the attacked models or replaced them if the damage was severe. When a model (including the wire) was not found, this record was considered as missing and a new model was placed on the tree. Like in the earlier experiments conducted in the same region (Kozlov et al. 2017; Zvereva et al. 2019), attacks by invertebrate predators on our models were extremely rare and therefore they have not been analysed.

2.4 Assessment of herbivory

On 8–16 August 2016–2019, when the majority of insect herbivores had completed their feeding, we haphazardly selected five mature individuals of each of the two birch species at each site. Each individual was located at least 10 m apart from others of its species. From each tree, we collected a branch with approximately 80–120 leaves (median value: 100 leaves). We avoided the impact of unconscious biases on the values of foliar losses by selecting the branches while standing at a distance of 5–10 m away, which prevented visual evaluation of leaf damage by insects. The branches were labelled with random numbers, so the person assessing herbivory was blinded with respect to the sample origin.

The leaves on each branch (including the petioles of fully consumed leaves) were counted, and each leaf was carefully examined for the presence of insect damage. Following a widely used methodology (Alliende 1989; Kozlov et al. 2015a), each leaf was assigned to one of the damage classes according to the percentage of the area of the leaf that was consumed or otherwise damaged by defoliating insects: 0 (intact leaves), 0.01–1, 1–5, 5–25, 25–50, 50–75 and 75–100%. The plant-specific percentage of foliage lost to insects was calculated as follows: the numbers of leaves in each damage class were multiplied by the respective median values 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. The abundances of *Eriocrania* and *Stigmella* leafminers were quantified as their intensities, i.e. the number of mines divided by the number of leaves on the branch.

2.5 Data analysis

We evaluated the explanatory power of latitude, MAT and MAP by comparing their correlations with all response variables by paired *t* test. The proportions of leafminers that died from different reasons and the proportions of attacked plasticine models were analysed using a generalised linear mixed model (Stroup 2013) with binomial error distribution and a logit link function with the event/trial syntax (procedure GLIMMIX; SAS Institute 2009). In the analysis of leafminer mortality, we considered the year as a fixed effect, latitude as a covariate, and the study site as a random intercept effect. In the analysis of bird predation on plasticine caterpillars, we added the colour and period of exposure as fixed effects.

The losses of birch foliage to chewing insects were analysed by mixed model ANCOVA, whereas intensities of leafminers were analysed using a generalised linear mixed model with binomial error distribution and a logit link function with the event/trial syntax. In these models, the year and birch species were treated as fixed effects, the latitude as a covariate, and the study site as a random intercept effect. The simultaneous involvement of both site and latitude in our analyses is justified by the fact that our sites differ not only in latitude, but also in a number of other characteristics (plant community structure, in particular).

To facilitate accurate *F* tests of the fixed effects, we adjusted the standard errors and denominator degrees of freedom in all our analyses by the latest version of the method described by Kenward and Roger (2009). The significance of a random factor was evaluated by calculating the likelihood ratio and testing it against the chi-squared distribution (as described in Littell et al. 2006).

The average mortality for each of three groups of leafminers (*Eriocrania* on birches, *Stigmella* on birches, and various moths on rowan) from each group of predators (birds and ants) and from unknown reasons was calculated for each site-by-year combination by dividing the number of individuals that died from respective reasons by the total number of collected mines. Similarly, the proportions of attacked plasticine models were calculated by dividing the numbers of attacked models by the total number of models at a site (attack rates hereafter). Mines that were killed by predators or that died from unknown reasons were excluded from the calculations of parasitism rates. The latitudinal patterns in mortality rates from different factors were explored by calculating the Pearson product-moment correlation coefficients between site-specific mortality rate and latitude separately for each study year and for each kind of prey. These individual correlation coefficients were combined in the subsequent meta-analysis.

2.6 Meta-analysis

We used meta-analysis to search for the general pattern in the data on latitudinal changes in herbivory levels and in different mortality factors of herbivorous insects. The attack rates on plasticine models were included in this analysis as a proxy for the mortality of defoliating caterpillars caused by birds. The effect sizes (ESs) were calculated by *z*-transforming the individual correlation coefficients and weighting them by their sample sizes. The mean ESs were computed and compared using the MetaWin 2.0 program (Rosenberg et al. 2000). The effect was considered statistically significant if the 95% confidence interval of the mean ES (CI_{95}) did not include zero. A negative ES indicated that the character decreased with an increase in latitude. The variation between years and groups of herbivores (categorical explanatory variables) was explored by calculating the heterogeneity index Q_B, which was tested against the chi-square distribution. All analyses were performed using random effects models.

3 RESULTS

3.1 Selection of the explanatory variable

The correlations of all response variables with MAT and MAP did not differ from their correlations with latitude (t_{12} = 0.24, P = 0.81 and t_{12} = 0.37, P = 0.72, respectively). The latitude explained a slightly larger part of variation in response variables (mean ± SE: R^2 = 0.176 ± 0.049) than MAT (0.167 ± 0.047) and MAP (0.134 ± 0.024) did.

3.2 Sources of mortality in leafminers

Most of the mortality factors in all groups of leafminers showed significant variations among the four study years (Fig. 2a-d, Tables S2–S4). Not every mortality factor-by-leafminer group combination demonstrated a significant effect of latitude, but the interaction between year and latitude was significant for all mortality factors for the *Eriocrania* miners and for three of the four mortality factors in a community of rowan leafminers (Tables S2, S3), indicating the common occurrence of among-year variation in latitudinal patterns. For example, *Eriocrania* mortality due to ant predation decreased in our gradient in 2016 and 2018, but not in 2017 and 2019 (Fig. 3a-d). Similarly, the mortality of *Eriocrania* larvae due to bird predation decreased with an increase in latitude in 2018 and 2019, but it did not correlate with latitude in either 2016 or 2017 (Fig. 3e-h). The mortality factors in *Stigmella* larvae on birches did not show any effects of year, or any year-by-latitude interaction; the effect of latitude was significant only for the parasitism level (Table S4).

3.3 Bird attacks on plasticine models

The proportion of caterpillar models attacked by birds varied among study years (Fig. 2a, Table S5) and study sites, but it did not differ between the green and brown models (Table S5). The correlation of bird attack rate with latitude also differed among study years, as indicated by the significant year-by-latitude interaction (Table S5). During two study years (2016 and 2019), no correlation was observed between bird predation and latitude, while in two other years (2017 and 2018), the bird predation rates decreased with increase in latitude (Fig. 3i-l).

3.4 Herbivory

The losses of birch leaf area to insect herbivores and frequency of *Stigmella* leafminers generally decreased with latitude (Fig. 4), but the strength of these changes varied among years, as indicated by significant year-by-latitude interactions (Tables S6 and S7). Across the study years, the losses of birch foliage to insects decreased from 10% to 3% between the southern and northern ends of the study gradient (Fig. 4).

3.5 General patterns in predation, parasitism and herbivory

Attacks by different groups of natural enemies (birds, ants and parasitoids) demonstrated different relationships with latitude (Table S8; $Q_B = 10.5$, df = 2, $P = 0.005$). The predation by birds and ants showed similar correlations with latitude (ES = -0.30 and ES= -0.21, respectively; $Q_B = 0.25$, df = 1, $P = 0.62$), indicating that the variation in latitudinal patterns among natural enemy groups was due to contrasting trends in predation and parasitism (ES = -0.26 and ES = 0.25, respectively; $Q_B = 10.4$, df = 1, $P = 0.001$). Across study years, predation (birds and ants combined) decreased towards the north, while parasitism increased with an increase in latitude (Fig. 5a, b). These trends were significant in three of the four years for both predation and parasitism (Fig. 5a, b). The overall impact from natural enemies (ES = -0.09, CI_{95} = -0.25…0.06), as well as the mortality of leafminers from unknown reasons (Fig. 5c), did not show any latitudinal changes. The latitudinal changes in bird predation did not differ between natural and artificial prey (ES = -0.21 and ES= -0.48, respectively; Q_B = 0.66, df = 1, $P = 0.42$). The foliar damage combined across all studied groups of birch herbivores decreased with increases in latitude (Fig. 5d).

4 DISCUSSION

4.1 Latitudinal changes in predation

The latitudinal gradients in different traits of biota, starting from the seminal work by Humboldt (1817), are generally associated with latitudinal changes in climate. However, the mechanisms behind this association could not be deciphered from observational studies because multiple abiotic and biotic factors change with latitude in a concerted manner (reviewed by De Frenne et al. 2013). Moreover, some latitudinal patterns may represent the legacy of the past effects of climate on the speed of evolution (Oppold et al. 2016). Therefore, in our study we focused on correlations with latitude, keeping in mind that a substantial part of latitudinal variation could be explained by climate.

The LBIH, which was originally developed for among-biome comparisons (Dobzhansky 1950; Schemske et al. 2009), has been verified by several macroecological studies of predation (Jeanne 1979; Roslin et al. 2017; Hargreaves et al. 2019). A few studies found a poleward decrease in predation rates within the temperate biome (Thompson & Ribic 2012; DeGregorio et al. 2016). Our study, despite considerable variations in latitudinal patterns among years and study systems, demonstrated that a significant overall decrease in predation pressure on herbivorous insects with increase in latitude also occurs within a boreal biome.

Most studies, both global and regional, found a decrease in predation by invertebrates from low to high latitudes. (Thompson & Ribic 2012; DeGregorio et al. 2016; Roslin et al. 2017; Zvereva et al. 2019). These latitudinal changes in predation are frequently associated with changes in the abundance of invertebrate predators (Roslin et al. 2017; Hargreaves et al. 2019). We suggest that the decline in ant predation in our latitudinal gradient was also driven mainly by a decline in ant abundance: analysis of the soil macrofauna in the same gradient showed a substantial poleward decrease in the density of predatory ants (M. Kozlov, unpublished data). The abundance of arboreal spiders considerably decreased along the same gradient (Kozlov et al. 2015b), indicating that different groups of arthropod predators demonstrate similar latitudinal changes.

Predation by vertebrates frequently shows latitudinal changes that contrast with the pattern in predation observed for invertebrates (Thompson & Ribic 2012; DeGregorio et al. 2016; Roslin et al. 2017; Zvereva et al. 2019). However, in our gradient, both bird and ant predation decrease with increases in latitude. Similarly to predation by ants, the poleward decrease in bird predation is consistent with the decrease in forest bird abundance. The counts of forest birds showed that their density in sites located at about 68ºN was 49% of their density in sites at 61ºN (calculated from supplementary data in Eeva et al. 2012). At the same time, this latitudinal pattern contradicts the results of the previous studies, which demonstrated either lack of latitudinal changes (Lövey & Ferrante 2017; Roslin et al. 2017) or even an increase in bird predation from low to high latitudes (Zvereva et al. 2019). However, the three latter studies reported global patterns, whereas we explored a relatively short gradient (ca 1000 km in length) crossing one biome. The observed controversy in the outcomes of the existing studies may indicate the possibility that latitudinal changes in biotic interactions across and within biomes are driven by different factors.

The similarity between the latitudinal patterns in bird attack rates on natural and standardized prey revealed by our study suggests that our natural prey does not show any latitudinal changes in anti-predator defence, which can potentially influence correlation between predation rate and latitude (Chen et al. 2017). This similarity also justifies the use of insect model prey in latitudinal studies of predation, which so far dominate this research field (Lövey & Ferrante 2017; Roslin et al. 2017; Zvereva et al. 2019). However, bird predation on natural and artificial prey showed some differences in both the average year-specific predation rates (Fig. 2a) and the among-year variation in latitudinal trends (Fig. 3e-l). These differences may be explained by differences in the sizes of our natural prey (5–10 mm in length) and the plasticine models (30 mm in length), because bird species, which differ in their preferences for prey size (Brandl et al. 1994), may show idiosyncratic among-year variations in abundance among our study sites.

4.2 Latitudinal changes in parasitism

The poleward increase in parasitism in leafmining herbivores was significant in three of the four study years (Fig. 5b). This finding is in line with a study by Rull et al. (2009), who revealed an increase in parasitism on apple maggot fly *Rhagoletis pomonella* from tropical to temperate deciduous forests. By contrast, several other studies did not find latitudinal changes in the parasitism rates of plant-feeding insects (Stireman et al. 2005; Moreira et al. 2015).

An increase in diversity with an increase in latitude has been demonstrated for many groups of parasitoid wasps (reviewed by Burington et al. 2020). This direction of the latitudinal diversity gradient is opposite to the pattern observed in a majority of taxa (Willig et al. 2003) and indicates that parasitoids demonstrate very unusual responses to environmental variations. For instance, the lack of a decrease in mortality from endoparasitoids at high latitudes may be explained by their life within host bodies, where they obtain partial protection from unfavourable environmental conditions (Hawkins 1994). This may be especially true for endoparasitoids of endophagous leafminers (Péré et al. 2013). The frequent occurrence of reciprocal patterns between predation and parasitism in between-site comparisons (Hawkins et al. 1997; Cornelissen & Stiling 2009; Libra et al. 2019) may result from the increase in parasitoid mortality with an increase in predation on parasitised hosts (Libra et al. 2019). Thus, herbivorous insects often escape one type of enemy only to succumb to another (Hawkins et al. 1997).

The opposite latitudinal changes in predation and parasitism result in changes in the relative contributions of different top-down factors to herbivore mortality from low to high latitudes. At the southern end of our gradient, the top-down factors are dominated by predation, while at the northern end of the gradient, the mortality of leafminers is caused mostly by parasitoids. Consequently, the overall impact of top-down factors on herbivores in our environmental gradient did not change with latitude. However, other study systems may show different patterns, depending on whether predation or parasitism is the leading mortality source for a particular herbivore. For example, the mortality from parasitism is lower in open-living insects than in concealed insects (Hawkins 1994). This may lead to a latitudinal decline in the overall top-down impact on open-living defoliators due to a higher contribution by predators to their mortality. Nevertheless, our study hints that a latitudinal trend in top-down pressure on herbivores can be revealed only if the impacts of all major groups of enemies are measured simultaneously.

4.3 Latitudinal changes in herbivory

Only a fraction of studies that have aimed at revealing latitudinal changes in herbivory have detected correlations with latitude (Moles et al. 2011a; Anstett et al. 2016). Furthermore, when a latitudinal pattern is discovered, the mechanisms behind it are rarely elucidated. The latitudinal gradients in insect herbivory have been suggested to arise due to a number of factors, including direct effects of climate on insect performance, abundance and diversity (Bale et al. 2002; Kozlov et al. 2013) and on the number of generations in some species (Yamamura & Kiritani 1998), the mechanical properties of the leaves (Onoda et al. 2011), plant defensive chemistry (Moles et al. 2011b) and natural enemy pressure (Björkman et al. 2011).

Björkman et al. (2011) argued that the impacts of both predators and parasitoids on herbivorous insects may contribute to latitudinal changes in herbivory. However, the lack of any overall latitudinal trend in the combined impacts of predators and parasitoids on herbivorous insects observed in our study indicates that top-down factors are unlikely to drive the latitudinal decline in birch herbivory that is consistently observed in our gradient (Kozlov 2008; Zverev et al. 2017; Zvereva et al. 2020; and this study). More studies from temperate and especially tropical regions are needed to draw justified conclusions regarding the contribution of top-down factors to latitudinal changes in insect herbivory.

The latitudinal decrease in herbivory is sometimes explained by an increase in antiherbivore plant defences from low to high latitudes (Moreira et al. 2018). However, the specific leaf area (SLA), which is frequently considered as a measure of mechanical defence, did not differ between birches growing at the opposite ends of our gradient (Zverev et al. 2017). Similarly, foliar concentrations of condensed tannins, which form the constitutive defence of *B. pubescens* against herbivores, did not show any latitudinal changes within the boreal forest zone (Stark et al. 2008). Therefore, we conclude that changes in leaf quality for herbivorous insects in our gradient are minor or non-existent, in line with several studies conducted in other regions (reviewed by Moles et al. 2011b). Moreover, the mortality of leafminers from unknown reasons, which reflects the level of plant antibiosis (Cornelissen & Stiling 2009; Hunter & Kozlov 2019), exhibits little or no latitudinal variation. All these data, taken together, suggest that bottom-up factors are also unlikely to drive the poleward decline in herbivory.

We therefore attribute the considerable poleward decline in birch herbivory in our study region to direct effects of temperature on insect populations (Bale et al. 2002) and on the consumption rates of herbivores (Lemoine et al. 2014). This opinion is indirectly supported by the significant correlation between plant losses to insects and the mid-summer temperatures, as revealed by earlier analyses of herbivory in our gradient (Kozlov 2008; Kozlov et al. 2013) and in other studies conducted at high latitudes (e.g. Rheubottom et al. 2019).

4.4 Among-year variations in latitudinal patterns in biotic interactions

The majority of published latitudinal studies are based on single-season measurements from each site (reviewed by Moles et al. 2011a; Anstett et al. 2016). The studies reporting latitudinal changes in the strength of biotic interactions during two or more years are infrequent for herbivory (e.g. Andrew & Hughes 2005; Kozlov 2008; Adams & Zhang 2009;

Zverev et al. 2017) and virtually non-existent for predation and parasitism on plant-feeding insects. This lack of multiyear data gives particular weight to the present study, which not only detected general trends in the impacts of top-down factors on natural populations of herbivorous insects across a four-year period but also revealed significant among-year variations in the strength of latitudinal changes. This variation was not consistent among interactions, objects and traits, and this inconsistency hampers identification of factors driving this variation. It is even possible that different factors are responsible for variations in different types of biotic interactions.

The among-year variation in latitudinal changes in the strength of biotic interactions may result from asynchronous fluctuations in population densities of animal groups under study, which may be driven by local factors. For example, the increase in plant damage in 2018 and 2019 likely emerged due to local outbreaks of some herbivore species in the sites located in the middle of our gradient. As the result, the latitudinal patterns in birch herbivory in these years deviated from the linear poleward decrease, which is typical for this gradient (Kozlov 2008; Zverev et al. 2017; and this study).

From a methodological perspective, our findings suggest that single-year latitudinal studies of biotic interactions may easily yield misleading conclusions. A single-year study, as seen from Fig. 3, would have only a 50% probability of detecting the existence of the latitudinal pattern in any of three illustrated characters (ant and bird predation on *Eriocrania* leafminers and bird predation on plasticine larvae). Therefore, we suggest that multi-year studies increase the probability of revealing the general patterns in biotic interactions, and that the proportion of studies that did not detect pattern predicted by LBIH would be much smaller if the data were collected during at least two study years.

CONCLUSION

Our findings considerably advance the knowledge of latitudinal patterns in biotic interactions by (i) identifying latitudinal patterns across time, (ii) disentangling latitudinal patterns across three enemy groups (birds, ants and parasitoids); (iii) revealing latitudinal pattern in overall natural enemy pressure on herbivorous insects; and (iv) demonstrating that measurements of bird predation on natural and artificial prey yield similar latitudinal patterns. We found that the strength of predator-prey interactions generally decreases with increases in latitude. This finding provides support for the LBIH and adds evidence to very limited information on the latitudinal patterns in predator impacts on herbivorous insects. Importantly, we revealed that the strength of these interactions decreases with increase in latitude not only at the global scale, but also within the single biome. At the same time, the strength of parasitoid-host interactions exhibits an opposite trend, i.e. it increases from low to high latitudes. Consequently, the overall pressure of natural enemies on herbivorous insects did not change with latitude. In combination with the absence of latitudinal changes in bottom-up effects, this finding suggests that direct effects of abiotic factors (climate, in the first line), rather than changes in the strength of biotic interactions, are what shapes the poleward decline in insect herbivory within the boreal forest zone. The considerable among-year variation in latitudinal patterns in herbivory, predation and parasitism calls for a wider use of multi-year data in studies that address spatial patterns in biotic interactions.

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AUTHOR’S CONTRIBUTIONS

ELZ and MVK jointly developed the study concept; VZ and MVK designed methodology and collected the data; MVK analysed the data; ELZ performed meta-analysis and wrote the first draft of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Should the manuscript be accepted, the data supporting the results will be archived in Dryad, and the data DOI will be included at the end of the article.

ORCID

Elena L. Zvereva https://orcid.org/0000-0003-2934-3421
Vitali Zverev https://orcid.org/0000-0002-8090-9235
Mikhail V. Kozlov https://orcid.org/0000-0002-9500-4244

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Figure captions

FIGURE 1 Study objects: a, mine of *Eriocrania* sp. on *Betula pubescens*; b, mine of *Stigmella lapponica* on *B. pubescens*; c, mine of *S. nylandriella* on *Sorbus aucuparia*; d, caterpillar-shaped plasticine model attached to a branch of *B. pubescens,* with several bird beak marks. Scale: 10 mm. Photo: V. Zverev (a-c) and E. Zvereva (d).

FIGURE 2 Among-year variation in predation by birds (a) and ants (b), parasitism (c) and mortality from unknown factors (d) in different groups of leafminers and in bird attacks on plasticine caterpillar models (a). Values are the estimated marginal means (+SE) from the SAS GLIMMIX procedure, based on data from 10 study sites. Bars with different letters indicate significant ($P < 0.05$) differences between study years (t-test from SAS GLIMMIX procedure).

FIGURE 3 Examples of among-year variation in latitudinal changes (r, Pearson correlation coefficient) in different interactions: ant predation rates on *Eriocrania* leafminers (a-d), bird predation rates on *Eriocrania* leafminers (e-h) and bird predation rates on plasticine models of caterpillars (i-l) from 2016-2019.

FIGURE 4 Latitudinal changes (r, Pearson correlation coefficient calculated for site-specific values averaged across four study years) in losses of birch foliage to chewing insect herbivores.

FIGURE 5 Overall and annual latitudinal trends in predation rate (bird and ant predation on various leafminers and bird predation on plasticine caterpillar models combined) (a), parasitism on various leafminers (b), leafminer mortality from unknown reasons (c) and insect herbivory on birches (d). The negative effect size values indicate a decrease in the interaction strength with increase in latitude. Horizontal lines denote 95% confidence intervals; sample sizes are shown in parentheses. For statistical analysis of among-year variation, see the text.

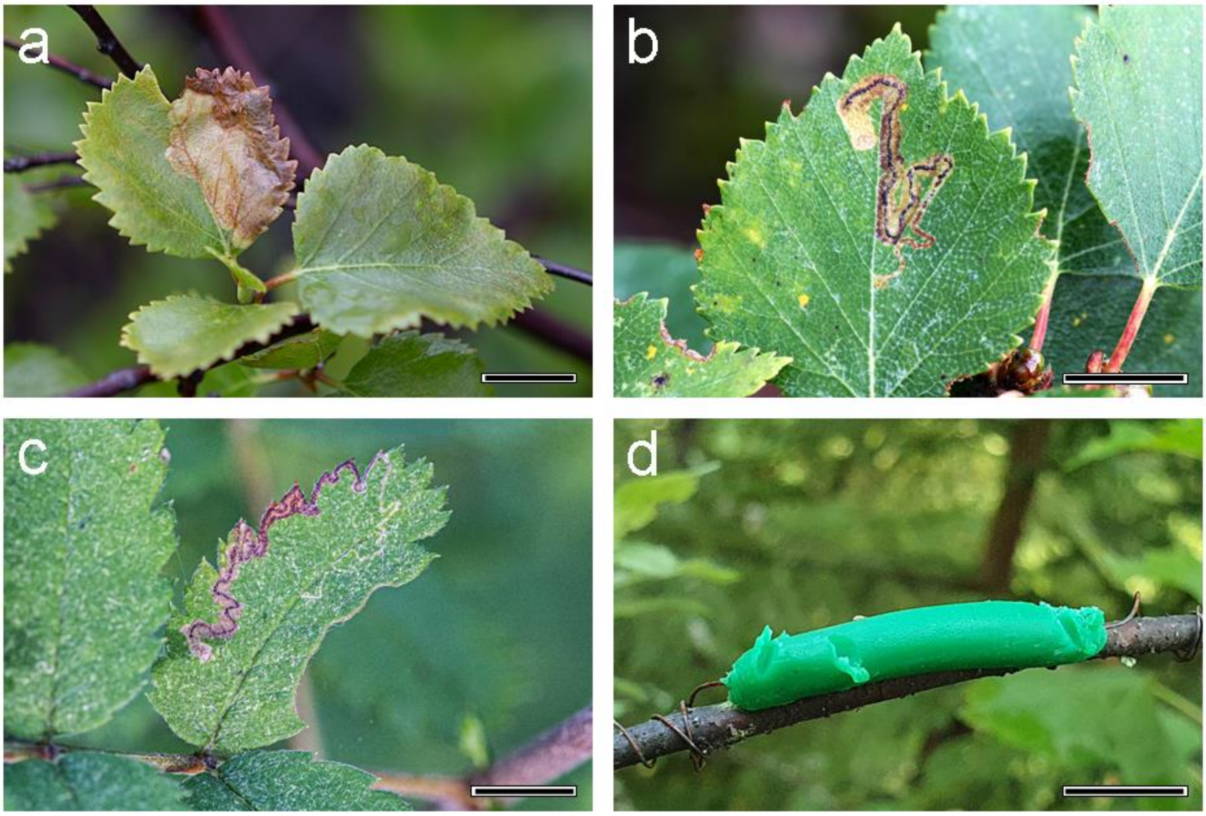
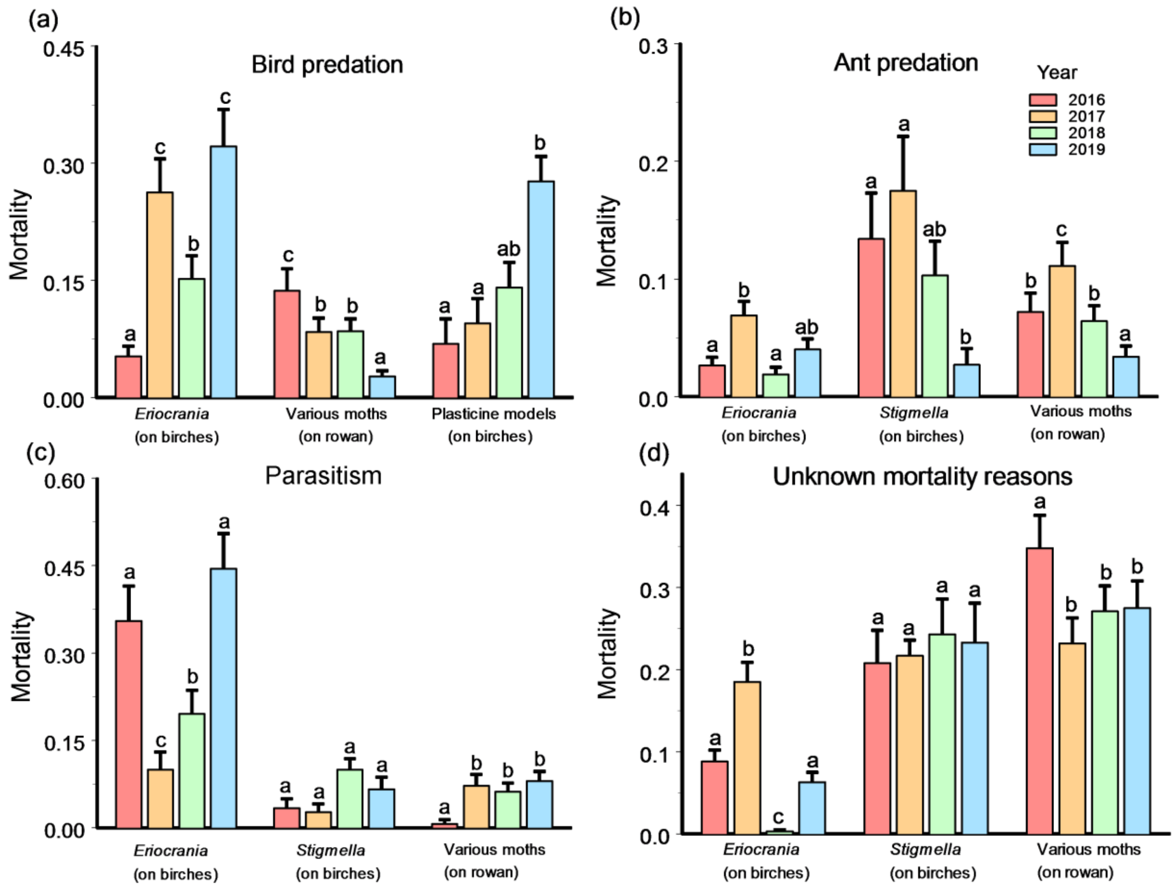


Figure 1



(a)
Bird predation
Mortality
0.45
0.30
0.15
0.00
a c b c
c b b a
a a ab b
Eriocrania (on birches)
Various moths (on rowan)
Plasticine models (on birches)
(b)
Ant predation
Year
2016
2017
2018
2019
Mortality
0.3
0.2
0.1
0.0
a b a ab
a a ab b
b c b a
Eriocrania (on birches)
Stigmella (on birches)
Various moths (on rowan)
(c)
Parasitism
Mortality
0.60
0.45
0.30
0.15
0.00
a c b a
a a a a
a b b b
Eriocrania (on birches)
Stigmella (on birches)
Various moths (on rowan)
(d)
Unknown mortality reasons
Mortality
0.4
0.3
0.2
0.1
0.0
a b c a
a a a a
a b b b
Eriocrania (on birches)
Stigmella (on birches)
Various moths (on rowan)

Figure 2

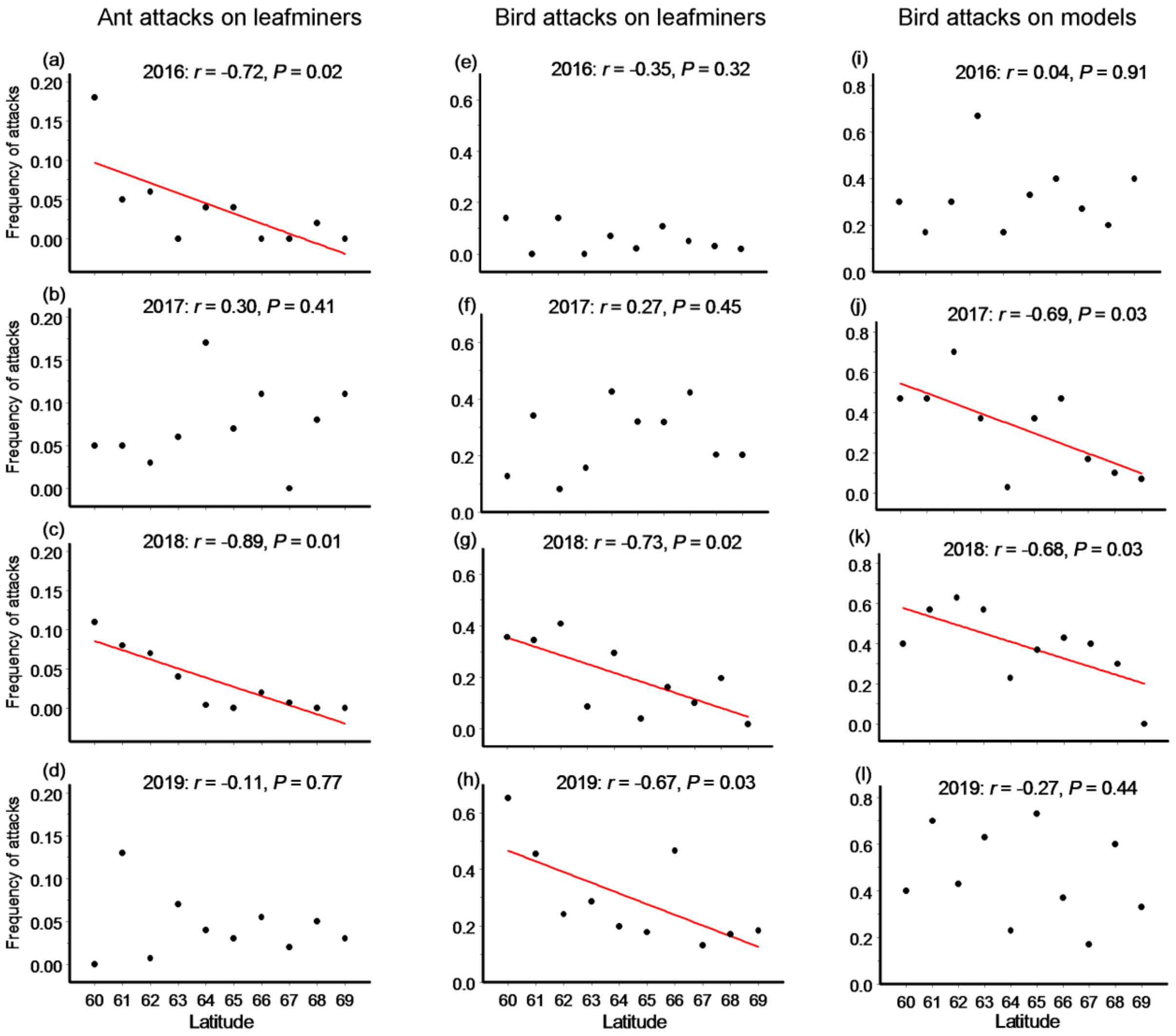

Ant attacks on leafminers
Bird attacks on leafminers
Bird attacks on models
(a)
2016: $r = -0.72$, $P = 0.02$
(b)
2017: $r = 0.30$, $P = 0.41$
(c)
2018: $r = -0.89$, $P = 0.01$
(d)
2019: $r = -0.11$, $P = 0.77$
(e)
2016: $r = -0.35$, $P = 0.32$
(f)
2017: $r = 0.27$, $P = 0.45$
(g)
2018: $r = -0.73$, $P = 0.02$
(h)
2019: $r = -0.67$, $P = 0.03$
(i)
2016: $r = 0.04$, $P = 0.91$
(j)
2017: $r = -0.69$, $P = 0.03$
(k)
2018: $r = -0.68$, $P = 0.03$
(l)
2019: $r = -0.27$, $P = 0.44$
Frequency of attacks
0.00
0.05
0.10
0.15
0.20
0.0
0.2
0.4
0.6
0.8
60 61 62 63 64 65 66 67 68 69
Latitude

Figure 3

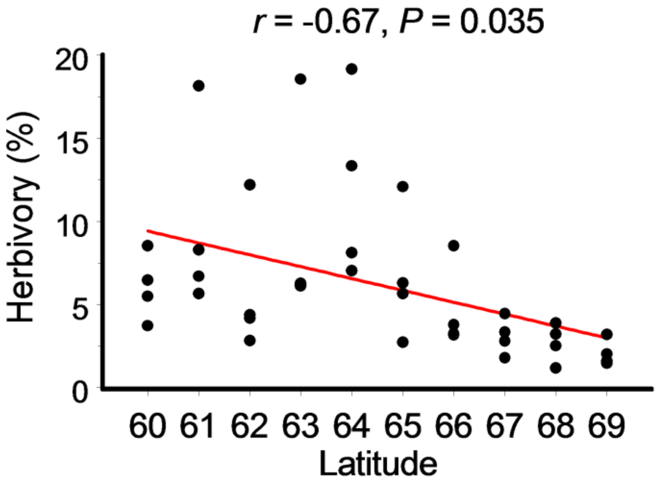

r = -0.67, P = 0.035
Herbivory (%)
20
15
10
5
0
60
61
62
63
64
65
66
67
68
69
Latitude

Figure 4

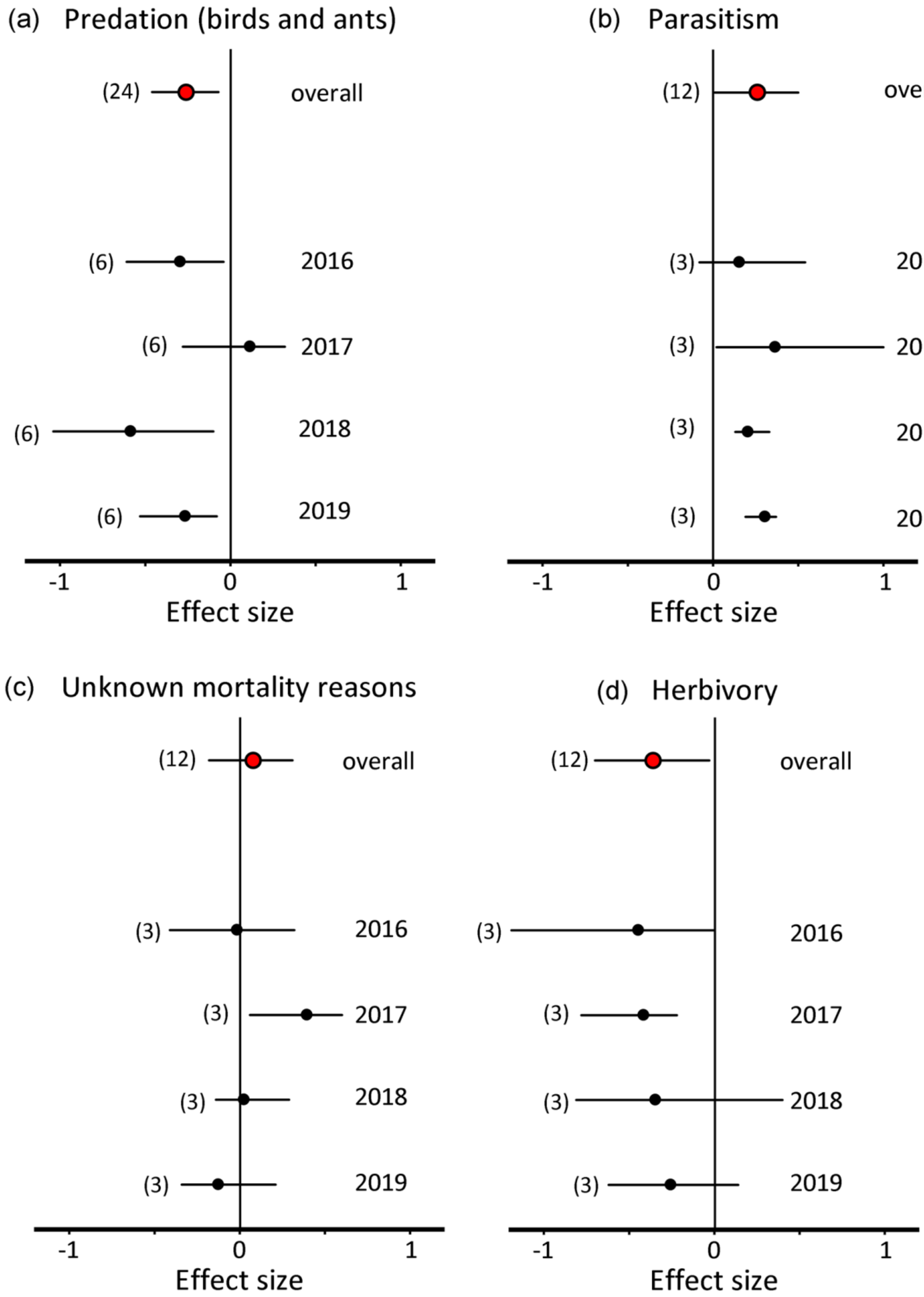

(a) Predation (birds and ants)
(24)
overall
(6)
2016
(6)
2017
(6)
2018
(6)
2019
-1
0
1
Effect size
(b) Parasitism
(12)
overall
(3)
2016
(3)
2017
(3)
2018
(3)
2019
-1
0
1
Effect size
(c) Unknown mortality reasons
(12)
overall
(3)
2016
(3)
2017
(3)
2018
(3)
2019
-1
0
1
Effect size
(d) Herbivory
(12)
overall
(3)
2016
(3)
2017
(3)
2018
(3)
2019
-1
0
1
Effect size

Figure 5