ORIGINAL PAPER

Bird predation does not explain spatial variation in insect herbivory in a forest–tundra ecotone

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

Abstract

The contribution of bird predation to the spatial variations in insect herbivory remains imperfectly understood, especially in Arctic ecosystems. We experimentally tested the hypothesis that the differences in insect herbivory between tundra and forest biomes, and between plant life-forms in these biomes, are associated with differences in the intensity of bird predation on defoliating insects. We observed substantial variation in herbivory (0% to 20% of foliage lost) among nine forest, mountain tundra, and lowland tundra sites in the Kola Peninsula (northwestern Russia) and among five woody plant species, but we found no consistent differences in herbivory between biomes and between plant life-forms. Bird attacks on artificial caterpillars were tenfold more frequent in forest than in tundra, while bird exclusion effects on herbivory did not differ between biomes, and the intensities of bird predation measured by these two methods were not correlated. Bird exclusion led to increases in insect herbivory, and this effect was significant in trees and tall shrubs but was not significant in dwarf shrubs in either forest or tundra sites. Bird predation, as measured in bird exclusion experiments, increased with an increase in the level of foliar damage inflicted by insects in forests but not in tundra habitats. We conclude that bird predation generally decreases plant losses to insects in both forest and tundra habitats, but birds are unlikely to shape the spatial patterns of plant losses to insects in Arctic ecosystems.

Keywords Artificial caterpillars · Biotic interactions · Bird exclusion · Kola peninsula · Plant life-forms

Introduction

Plant damage by herbivores greatly varies in both space and time. The most widely debated patterns in insect herbivory concern differences between latitudes (Adams and Zhang 2009; Kozlov et al. 2015a; Lim et al. 2015), altitudes (Galmán et al. 2018), plant life-forms (Kozlov et al. 2015c; Lim et al. 2015), and plant ontogenetic stages (Barton and Koricheva 2010; Zverev et al. 2017). Numerous hypotheses have been proposed to explain some of these patterns, but one hypothesis in particular focuses on the importance of natural enemies, especially predators, and implicitly assumes

that the impact of predators on herbivores varies along environmental gradients (Björkman et al. 2011; Roslin et al. 2017). This hypothesis, in turn, is based on the influential 'green world' hypothesis, which states that herbivores do not consume all their food supplies because predators effectively control herbivore populations (Hairston et al. 1960; Polis, 1999). A more balanced opinion is that herbivore densities are determined by an interplay of bottom-up and top-down forces (Hunter and Price 1992; Gripenberg and Roslin 2007; Hunter and Kozlov 2019); however, bottom-up factors, primarily plant defenses (Karban and Baldwin 1997; Hunter 2016), have been explored much more intensively during the past decades than have the top-down factors. Nevertheless, the number of studies addressing effects of predation on herbivory in different environments is increasing rapidly (Roslin et al. 2017; Zvereva et al. 2019).

Birds are the most important generalist vertebrate predators of herbivorous insects. The importance of birds in protecting forests from insect damage was proved scientifically about a century ago (reviewed by Bruns 1960; Inozemtsev 1978), and meta-analysis of controlled experiments has

✉ Mikhail V. Kozlov
mikoz@utu.fi

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

confirmed that birds generally reduce plant losses to insects (Mäntylä et al. 2011). However, the intensity of bird predation on plant-feeding insects may differ between habitat types (Inozemtsev 1978; Garibaldi et al. 2010; Ruiz-Guerra et al. 2017), between sites (Connor et al. 1999; Brewer and Gaston 2003), and between plant species within a site (Holmes and Robinson 1981; Giffard et al. 2012; Singer et al. 2012); as the result, the actual contribution of bird predation to the observed variation in insect herbivory at different scales remains unclear. Even more importantly, the data available so far do not allow for prediction of the sign of correlation between bird's predation and insect herbivory: not only does bird impact decrease abundance of plant-feeding insects (Mäntylä et al. 2011), but low insect availability also decreases abundance of insectivorous birds (Martin 1987; Thiollay 1988).

Bird impacts on plant-feeding insects can be assessed by different methods. Among them, bird exclusion experiments yield a direct measure of the intensity of bird predation on prey, but the experiments themselves are quite laborious and time-consuming. Furthermore, due to the risk of vandalism, these experiments are difficult to arrange in densely populated areas. This explains why growing numbers of researchers now use artificial caterpillars to quantify bird predation rates on insects (Richards and Coley 2007; Howe et al. 2009; Tvardikova and Novotny 2012; Kozlov et al. 2017; Roslin et al. 2017). However, studies are still needed to confirm that the patterns of bird attacks on prey dummies translate into patterns of bird predation on plant-feeding insects and, subsequently, into patterns of plant losses to insects.

Our previous work demonstrated considerable differences in the losses of woody plant foliage to insects between forest and tundra biomes (i.e., along latitudinal gradient) and between trees (or relatively tall shrubs) and dwarf shrubs within both these biomes (Kozlov et al. 2015a, b, c). These differences identified the forest–tundra ecotone as a suitable area for comparative studies of bird impacts on insect herbivory, particularly due to great difference between the adjacent biomes. Moreover, to our knowledge, bird effects on insect herbivory have never been explored in a tundra site, despite the commonly appreciated importance of elucidating the ecological processes in this rapidly changing biome.

We experimentally tested the hypothesis that the differences in insect herbivory between forest and tundra biomes, and between trees and dwarf shrubs in these biomes, are at least partly explained by differences in the intensity of bird predation on defoliating insects. We predicted that (i) bird exclusion will increase plant losses to insects, (ii) the effects of bird exclusion on losses of plant foliage to insects increase with the baseline level of herbivory in the study area (measured in plants protected from bird predation), i.e. are positively density-dependent, (iii) bird predation on artificial caterpillars differs between biomes and between plant life-forms, and that (iv) two commonly used methods, bird exclusion and use of artificial caterpillars, show similar spatial patterns of bird predation.

Materials and methods

Study area and study sites

The study was conducted in the Kola Peninsula, in northwestern Russia, a region that provides a unique opportunity to compare ecological processes in forests with those in both mountain and lowland tundra within a relatively small geographic area (Fig. 1). The southern part of the study region, which lies about 100 km south of the northern tree limit, is covered by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) forests. Both latitudinal (at about 69° N) and altitudinal (at about 350–450 m a.s.l.) tree lines are formed by sparse, low-stature woodlands of mountain birch (*Betula pubescens* var. *pumila* (L.) Govaerts). Field-layer vegetation in the forest and tundra sites consists primarily of crowberry, *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, bilberry, *Vaccinium myrtillus* L., and lingonberry, *Vaccinium vitis-idaea* L. (Online Resource, Fig. S1).

The summer in our study region is cool and short, lasting from 2 to 3 months. The mean temperature in January in our sites ranges from -11 to -14 °C and in July from $+11$ to $+14$ °C, with an annual precipitation from 450 to 560 mm. The frost-free period varies from 50 to 100 days, but snow may occasionally occur even in mid-summer.

The study was replicated at four hierarchical levels (biomes, sites, plant life-forms, and plant species). We used nine study sites; three were located in wet spruce forests near
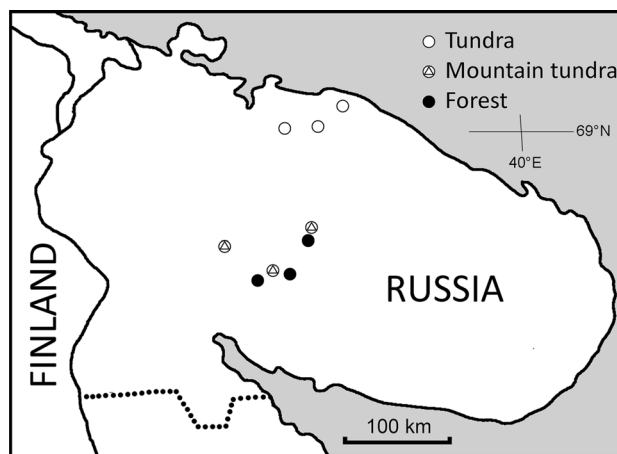

Fig. 1 Positions of study sites within the Kola Peninsula, northwestern Russia. For coordinates of sites, consult Online Resource, Table S1

Revda, Apatity, and Koashva, three were in alpine tundra on different mountain ranges (the Lovozero Mts., Monche-Tundra Mts., and Khibiny Mts.), and three were in lowland tundra along the road from Murmansk to Dalnie Zelentsy (Fig. 1; Online Resource, Table S1). The use of mountain tundra sites, which are interspersed within the forested area, allowed distinguishing latitudinal effects from differences between biomes (forest and tundra). Within each site, we measured insect herbivory and bird predation on mountain birch and willows (*Salix glauca* L. or *S. phylicifolia* L., depending on their availability at different sites) as two relatively high-stature woody plant species (trees and shrubs, conventionally called trees hereafter) and on bilberry and lingonberry as two low-stature species (dwarf shrubs, hereafter). Based on tree/shrub density and cover of field-layer vegetation (unpublished data), we estimate that, on average, foliar biomass of our study species in tundra and mountain tundra sites was 1–10% of that observed in forest sites.

Effects of bird exclusion on insect herbivory

We quantified bird predation pressure on herbivores as the difference in losses of plant foliage to insects between bird-excluded and control plants or branches. Before budbreak in spring 2017, we selected six mountain birch and six willow individuals, six patches of bilberry, and six patches of lingonberry at each site. A patch of dwarf shrub was defined as a group of stems growing in an area at least 20×20 cm in size and expected to produce no fewer than 100 leaves in the coming summer. The birds were excluded from one half of the experimental plants/patches with dark green bird netting (20 mm grid; Rastasverkko Pienisilmäinen, Tarha-tuote Oy, Finland). This type of netting does not prevent insect access to plants (Sipura 1999), but it does not allow birds to feed on insects on the protected plant. For trees, we covered the entire plant or a large branch with the same type of netting. The exclosures over dwarf shrub patches were established using Π-shaped stands made of strong wire, which supported the netting above the plants (Online Resource, Fig. S1). In total, we established 108 exclosures, i.e. 12 exclosures in each of nine study sites.

In the autumn of 2017, 2 weeks before the beginning of leaf fall, we haphazardly collected branches/stems (for a total of at least 100 leaves) from the central part of each exclosure and from each control plant/patch. Recent meta-analysis demonstrated that haphazard selection of a control branch was unlikely to cause bias in our estimates of plant losses to insects (Zvereva and Kozlov 2019). In the evergreen lingonberry we considered current-year leaves only. Each collected leaf was attributed to one of the following damage classes according to the percentage of the leaf area that was consumed or damaged (mined or skeletonized) by insects: intact leaves; 0.01–1; 1.1–5; 6–25; 26–50; 51–75;

and 76–100%. The number of leaves in each damage class was then multiplied by the median value of the damaged leaf area (i.e., 0.5% for the damage class 0.01–1%) and the obtained values were summed for all damage classes within a sample and divided by the total number of leaves (including undamaged ones). This method, which returns the average percentage of leaf area lost to (or damaged by) leaf-chewing insects, is widely used in studies of insect herbivory (reviewed by Kozlov and Zvereva 2017). The visual assessment of herbivory is less laborious than the analysis of leaf images, which in particular requires manual reconstruction of the edge of each damaged leaf; these two methods do not differ in either the accuracy of measurements (Johnson et al. 2016) or in the size of the reported effects of different environmental factors on insect herbivory (Zvereva and Kozlov 2019).

Bird attack rates on artificial caterpillars

For this experiment, we used artificial caterpillars of about the same size and shape as were used by many other researchers (Howe et al. 2009; Roslin et al. 2017). They were made from soft modelling clay announced to be nontoxic and odorless (Chemical plant "Luch," Yaroslavl, Russia). Two artificial caterpillars (approximately 30 mm length and 4 mm diameter) of different cryptic colors (green and brown, reflecting most common natural prey colors in our study area) were attached by fine dark green wire (0.3 mm diameter) just before budbreak (in June of 2017) to three individuals of each of the four selected plant species at each study site. On trees, the caterpillars were attached 30 to 60 cm apart on branches 4–8 mm in diameter, at a height of 1–2 m above the ground. On dwarf shrubs, the caterpillars were attached 30 to 200 cm apart, to stems 2–6 mm in diameter, at 0–15 cm above the ground (Online Resource, Fig. S1c). In total, we used 216 artificial caterpillars, i.e. 24 caterpillars per each of nine study sites. We checked for the signs of predator attacks on these artificial caterpillars during the third week of August 2017, which was 47–54 days after their deployment. At this time, the majority of herbivores completed their feeding in our study region. In terms of the number of dummy caterpillars per plot and of their total exposure time our experiment was similar to the currently published global study (Roslin et al. 2017).

Statistical analyses

The proportions of leaf area lost to leaf-chewing insects were transformed as $\ln(1 + \sqrt{x})$ and analyzed by a mixed-model ANOVA (procedure GLIMMIX; SAS Institute 2009). Numbers of artificial caterpillars attacked by birds were analyzed using a generalized linear mixed model (procedure GLIMMIX in SAS; binomial distribution and

the events/trials syntax). In both these analyses, the habitat (tundra, mountain tundra, and forest), plant life form and their interactions were considered fixed effects and a site was considered a random effect. In the analysis of herbivory, we also included treatment (bird exclusion) as a fixed effect and plant species as a random effect. We facilitated accurate F tests of the fixed effects by adjusting the standard errors and denominator degrees of freedom using the latest version of the method by Kenward and Roger (2009). The significance of random effects was tested by a likelihood ratio test (Stroup 2013).

In addition to a mixed model ANOVA, we used a meta-analytic approach, as we had in an earlier study (Kozlov et al. 2017), for the analysis of the outcomes of bird exclusion experiments. For each pair of samples (i.e., treatment and control for each plant species × site combination), we calculated a Hedge's d measure of the effect size (ES) as the difference between the mean percentage of leaf area lost to insects in three branches/patches covered by the netting and three control branches/patches, divided by the pooled standard deviation and weighted by the sample size. A positive ES indicates that losses of plant foliage to insects are greater in the enclosed plants than in the control plants.

The mean ESs were computed and compared using the METAWIN 2.0 program (Rosenberg et al. 2000). Bird exclusion was considered to have a statistically significant effect on herbivory if the 95% confidence interval of the mean ES did not include zero. The variation in the ESs among classes of categorical variables (habitats, plant species, and plant life-forms) was explored by calculating the heterogeneity index (Q_B), and the variation associated with changes in the continuous variable (herbivory measured in plants protected from bird predation) was evaluated by calculating Q_M and the slope of meta-regression. Both these indices were tested against the chi-square distribution. All analyses were performed using random effects models.
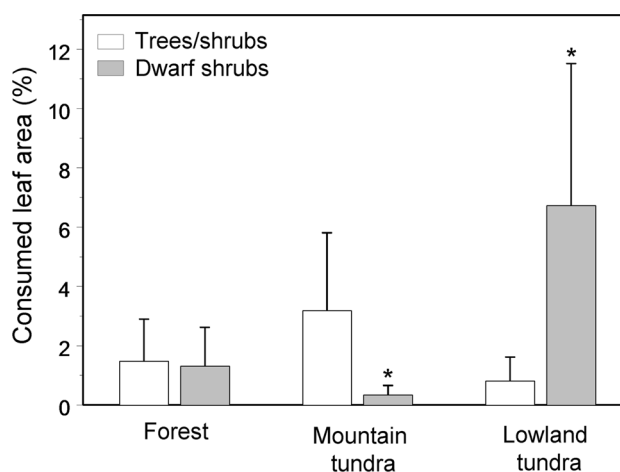

Fig. 2 The average levels of foliar damage (estimated marginal means + S.E.) caused by defoliating insects in control plants by the end of the experiment. An asterisk indicates significant ($P \leq 0.05$) within-habitat difference between plant life-forms

Results

Effects of bird exclusion on plant losses to insects

The losses of foliage to insects, measured in control plants, ranged from 0.04 to 20% (Online Resource, Fig. S2; averaged by plant species × study site). A vast majority of leaf damage was imposed by externally feeding chewing insects, primarily moth, sawfly, and beetle larvae. Across the entire experiment (including both control plants and plants protected from bird predation), the level of foliar damage showed habitat-specific differences between plant life-forms (habitat × plant life form interaction in Table 1). In forests, we found no differences in foliar damage inflicted by insects between trees and dwarf shrubs. In mountain tundra, the losses to insects were five times greater for trees than for dwarf shrubs, whereas in lowland tundra the insect damage was four times more intensive on dwarf shrub foliage than on tree foliage (Fig. 2). The levels of herbivory also varied among the study sites and among plant species (Table 1).

Table 1 Sources of variation in losses of woody plant foliage to insects (mixed-model ANOVA, SAS GLIMMIX procedure, type III tests)

Effect type	Source of variation	Test statistics	P value
Fixed	Habitat	$F_{2,12.65} = 2.35$	0.14
	Plant life form	$F_{1,2.80} = 0.18$	0.70
	Habitat × plant life form	$F_{2,195.5} = 44.9$	< 0.0001
	Bird exclusion	$F_{1,194.6} = 4.11$	0.04
	Bird exclusion × habitat	$F_{2,194.6} = 0.08$	0.93
	Bird exclusion × plant life form	$F_{1,194.6} = 2.13$	0.15
	Bird exclusion × habitat × plant life form	$F_{2,194.6} = 0.69$	0.50
Random	Site	$\chi^2_1 = 47.8$	< 0.0001
	Plant species	$\chi^2_1 = 21.8$	< 0.0001

Bird exclusion, on average, increased losses of plant foliage to insects by one-third of the control level, from 1.92 to 2.59%, and this effect was consistent across habitats (Table 1). In addition to variation discovered by ANOVA (Table 1), meta-analysis of the differences in herbivory between control plants and plants protected from birds within a site revealed that bird exclusion increased leaf damage by insects in trees, but not in dwarf shrubs, in all types of habitats (Fig. 3). Foliar losses to insects in bird-excluded trees increased in forests by a factor of three (median value), and in tundra by a factor of one-and-half relative to control plants.

Bird predation pressure on herbivores increased with an increase in the level of damage inflicted by insects in bird-excluded plants in forest habitats (Fig. 4a; meta-regression: $Q_M = 3.88$, $P = 0.049$), but showed no dependence on it in tundra habitats (Fig. 4b; $Q_M = 0.42$, $P = 0.51$).

Bird attack rates on artificial caterpillars

Eighteen of the 216 artificial caterpillars had beak marks, i.e. were attacked by birds during the time of exposure (50 days, on average). Three dummy larvae attached to dwarf shrubs were damaged by small mammals (two in forests and one in tundra). We did not observe any marks on the plasticine that could be attributed to invertebrate predators.

The frequency of bird attacks on artificial caterpillars did not differ between lowland and mountain tundra ($F_{1,68} = 0.01$, $P = 0.98$); therefore, the data collected in these two habitat types were combined and contrasted with the data from forests. The number of artificial caterpillars with beak marks was ten times higher in forests than in tundra ($F_{1,4} = 8.95$, $P = 0.040$), but the differences between plant life-forms were habitat-specific (interactive effect: $F_{1,100} = 4.05$, $P = 0.047$). In forests, birds attacked artificial caterpillars attached to tree branches six times more frequently than they attacked larvae attached to dwarf shrub stems. By contrast, in tundra, the attack rates to dummies attached to all plants were similar and low (Fig. 5). The frequency of bird attacks did not vary among the study sites nested within habitats ($\chi_1^2 = 0.00$, $P = 0.99$) and did
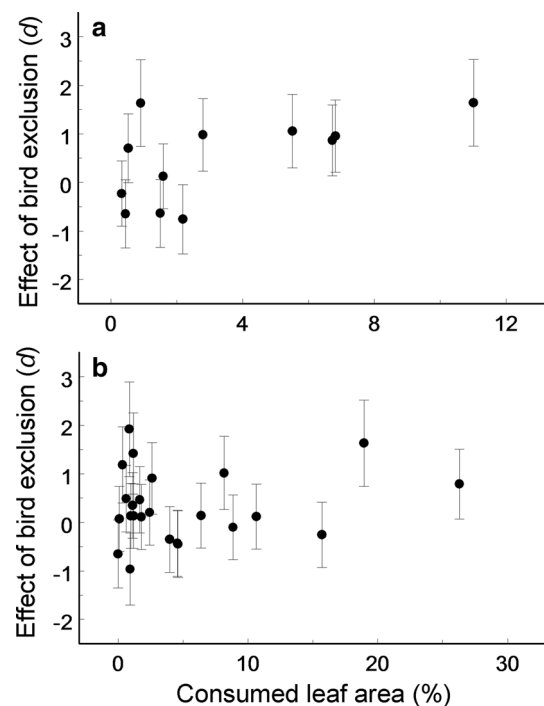
Fig. 4 Effect of bird exclusion (Hedge's $d \pm$ variance calculated for each plant species by site combination) plotted against the level of herbivory (measured from plants protected from birds) in forest (**a**) and tundra (**b**) habitats. For statistics, see text

not correlate with the effects of bird exclusion on insect herbivory in either forest ($Q_M = 0.44$, $P = 0.51$) or tundra habitats ($Q_M = 0.04$, $P = 0.83$).

Discussion

Differences in bird impacts on insect herbivory between biomes

In this study, the effects of bird exclusion on losses of plant foliage to insects did not differ statistically between the forest and tundra biomes, in line with the conclusion

Fig. 3 Sources of variation in effects of bird exclusion on foliar losses of woody plants to defoliating insects. The positive effect size values indicate that plants protected from birds suffered higher leaf damage by insects than plants exposed to birds. Horizontal lines denote 95% confidence intervals; sample sizes in parentheses; and Q_B refers to among-group comparisons
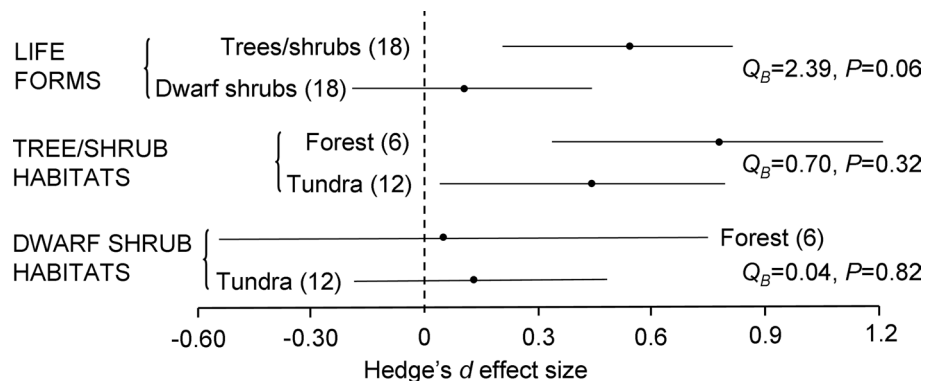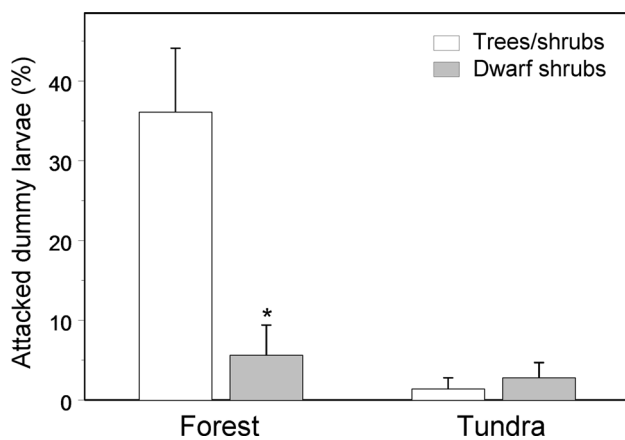
Fig. 5 Percentage of artificial caterpillars (estimated marginal means + S.E.; sample sizes: forest, 72 caterpillars; tundra, 144 caterpillars) attacked by birds during the experiment. An asterisk indicates significant ($P \leq 0.05$) within-habitat difference between plant life-forms

by Mäntylä et al. (2011). At the same time, birds attacked, on average, ten times more artificial caterpillars in our forest sites than in the tundra sites, and 25 times more if the comparison was restricted to trees. This finding disagrees with the results from the earlier study (Roslin et al. 2017), which did not detect any difference between biomes (including forest and tundra) in bird attack rates on artificial caterpillars. However, both our study and study by Roslin et al. (2017) were conducted during the single growth season, which poses limitations to interpretation of the discrepancies between studies.

The between-biome difference in the bird predation pressure on insect herbivores did not reach the level of statistical significance due to the extreme within-biome variation. Nevertheless, the strength of bird impacts on losses of tree foliage to insects in tundra was, on average, half of that in forests. The multiyear observations (Bianki et al. 1993) revealed that an average density of arthropod-feeding birds in the tundra of the Kola Peninsula was about one half that in the forests. We, therefore, conclude that the bird exclusion experiments provide a more realistic estimate of the difference in bird impacts on insect herbivory between forest and tundra than was obtained by artificial caterpillar experiments.

Differences in bird impact on insect herbivory between plant life-forms

The bird exclusion experiments and the bird attack rates on artificial caterpillars both indicated a higher intensity of bird predation on trees than on dwarf shrubs in forest sites. This observation agreed with the findings of Loiselle and Farji-Brener (2002), who reported that artificial caterpillars were

attacked by forest birds in tree canopies but not in the understory. The results of that study and of the present one may be explained at least partly by the greater numbers of bird species that forage in tree canopies than in low vegetation strata in various forest habitats (Mac Nally 1994; Korňan et al. 2013; González-Salazar et al. 2014). In the forests of the Kola Peninsula, 29 bird species that include arthropods in their diet show a preference for foraging in tree canopies, whereas 17 species search for their food mostly on the ground and sometimes on field-layer vegetation. Moreover, the total abundance is two times higher for the first group of bird species than for the second group (as calculated from data published by Bianki et al. 1993).

Intriguingly, bird exclusion significantly increased insect herbivory in trees not only in the forests but also in the tundra sites, where birch and shrubby willows were sparse (one tree/shrub per 500–5000 m^2: Online Resource, Fig. S1). Trees were clearly preferred by foraging birds over the continuous cover of dwarf shrubs, even when herbivore insects were much more abundant on dwarf shrubs than on birches and willows, as in our lowland tundra sites. One possible explanation is that 77% of the bird species of the tundra habitats of the Kola Peninsula were also found in the forest habitats (Bianki et al. 1993), and these tundra residents may still maintain their preference for foraging in tree canopies. In addition, the intensity of bird foraging on plant-feeding insects greatly depends on the foliage structure of the plant species (Holmes and Robinson 1981; Wood et al. 2012). Trees and dwarf shrubs differ greatly in many structural traits, including height, thickness of branches, and leaf size, and these differences may be partly responsible for the differences in the bird predation pressure on herbivores found between plant life-forms in our study.

The absence of any effects of bird exclusion on insect herbivory in dwarf shrubs within our forest sites contrasts with earlier reports showing an increase in bilberry damage by defoliating larvae following bird exclusion (Atlegrim 1989; Strengbom et al. 2005). The reason for these contradictory findings remains to be identified. The previous experiments were conducted in forests 450–600 km to the south of our study sites, raising the possibility that the bird foraging rate on insects feeding on dwarf shrub foliage decreases with an increase in latitude. Alternatively, the differences between outcomes of these experiments could have arisen due to some other as yet unknown factor.

Bird predation measured using artificial caterpillars vs. exclusion experiments

Researchers generally appreciate that numerous methodological problems are associated with the use of artificial caterpillars for measurements of bird predation intensity (Lövei and Ferrante 2017; and references therein). Nevertheless,

one common assumption is that, provided the experimental setups are similar, the attack rates on artificial caterpillars reflect among-habitat differences in predation pressure on insect herbivores (Richards and Coley 2007; Howe et al. 2009; Tvardikova and Novotny 2012). However, in our study, the 25-fold difference in attack rates on artificial caterpillars on trees between forest and tundra sites did not match either the two-fold difference in increases in insect herbivory following bird exclusion or the two-fold difference in bird density. Consistently, meta-regression demonstrated that the impacts of bird predation on losses of plant foliage to insects across tundra and forest sites could not be predicted from the rate of bird attacks on artificial caterpillars attached to branches of plants at these sites. Thus, if we depended on the data obtained for bird's attacks on artificial caterpillars, we would considerably overestimate the differences in bird predation pressure on herbivores between biomes and between plant life-forms within the tundra biome.

The great discrepancy between the results obtained by the two different methods commonly used to measure bird predation may lie in the different compositions of the insect prey communities in the tundra and forest sites. We suggest that, due to extremely low density of trees and tall shrubs in tundra sites, the abundance of large cryptic larvae that in our region feed almost exclusively on tree foliage is much lower in tundra than in forests, and birds living in tundra are less familiar with this kind of prey than are birds living in forests. Birds need to undergo some learning to discriminate the visual features of their prey (Curio 1976); therefore, tundra birds that only rarely encounter large larva may not recognize artificial caterpillars as a suitable food, or the tundra birds may even experience neophobia towards our models. In general, insectivorous birds commonly exhibit negative frequency-dependent predation and disproportionately select the more abundant prey types, while overlooking rarer ones (Tinbergen 1960; Allen 1988; Bond and Kamil 2002).

We suggest that the outcomes of studies that use model prey to measure the impacts of visually hunting predators on prey population will depend on the abundance of the natural prey (i.e., the prey being modeled) in the study sites. This suggestion is indirectly supported by the consistency between the results of bird exclusion experiments and the experiments involving artificial larvae exposure in one of the two within-biome comparisons (plant life-forms in forests, where caterpillars matching the size of our models are relatively common), whereas no consistencies were found in among-biome and among-site comparisons. Thus, conclusions on the relative intensity of top-down forces acting on plant-feeding insects in different environments, which have been based exclusively on measurements of bird attack rates on dummies (e.g., González-Gómez et al. 2006; Seifert et al. 2015; Roslin et al. 2017), may be flawed. In particular, a cross-biome comparison of bird consumption of arthropod

prey reported 25-fold differences between Arctic tundra and tropical forests (Nyffeler et al. 2018), whereas the study based on artificial caterpillars revealed no latitudinal trend in attack rates by birds (Roslin et al. 2017). More rigorous experimental studies that simultaneously measure predator impacts on artificial and natural prey (e.g., Kozlov et al. 2017, Ruiz-Guerra et al. 2017) are badly needed to validate earlier work and to justify the further use of dummies in ecological and environmental research.

The levels of insect herbivory and effects of bird exclusion

We observed a substantial variation in herbivory among our study sites, between plant life-forms in the tundra sites, and among plant species, with a foliage loss to insects that ranged from nearly 0% to ca. 20%. Within this range of plant damage, the effects of bird predation on insect herbivory did not explain either the current-year (Fig. 2) or the long-term (Kozlov et al. 2015a, b, c) differences in herbivory between biomes and between plant life-forms.

At the same time, our results indicate that the intensity of bird predation on insect herbivores increased in forest habitats with the increase in the potential level of herbivory, whereas no such correlation was detected in tundra habitats. In other words, bird predation showed positive density dependence on the abundance of defoliating insects and can, potentially, regulate their densities in Subarctic forests but not in tundra, either lowland or mountain. This difference in the expression and direction of density dependence between habitats is in line with the variation among outcomes of earlier studies, which reported both positive (Itämies and Ojanen 1977; Singer et al. 2012) and negative (Heads and Lawton 1983; Connor et al. 1999) spatial density dependence of bird predation on plant-feeding insects at different scales, from individual leaves (Connor et al. 1999) to entire study sites (Itämies and Ojanen 1977), or discovered no correspondence between herbivore abundance and the strength of bird predation (Champlin et al. 2009; Schwenk et al. 2010). The reasons underlying this variation remain in question, because even the studies of bird predation on the same herbivore species (Heads and Lawton 1983; Brewer and Gaston 2003) yielded inconsistent conclusions concerning spatial density dependence. One explanation may be that different bird species respond differently to prey abundance; for example, Holmes and Schultz (1988) found that six of ten bird species directed attacks to substrates in proportion to the abundance of the moth larvae present, while the other four species did not respond in the same way because they preferred other kinds of prey.

The absence of the anticipated correlation between the levels of insect herbivory and bird predation effects on insect herbivory in tundra habitats may simply result from lower

density of insectivorous birds relative to forest habitats (Bianki et al. 1993) and, consequently, from lower overall consumption of herbivorous insects (Nyffeler et al. 2018). The same effect may also arise from the flexibility of birds to adjust their diets to their current situation: insectivorous birds are not limited to consuming defoliating insects and can ingest a variety of prey species (e.g., Holmes and Schultz 1988). For example, in Subarctic forests of the Kola Peninsula, spiders comprised 75% of the food biomass brought by Siberian tits, *Parus cinctus*, to nestlings, whereas the biomass contributed by defoliating insects to this food was approximately 15% (Zatsarinnyi et al. 2014). In the same region, the European pied flycatcher, *Ficedula hypoleuca*, brought a more diverse food to nestlings, with defoliating insects contributing 2–20% of the biomass in different years (Gilyazova 1999). This diet breadth served as the basis of the hypothesis erected long ago (Howard and Fiske 1911) that birds, due to generally density-independent predation, are unlikely to affect the population dynamics of plant-feeding insects, especially at background (i.e., non-outbreak) levels of insect density.

Conclusions

We provide the first demonstration that the impact of insectivorous birds on defoliating insects may differ between plant life-forms within a habitat. Bird predation had a significant impact on herbivory on trees and shrubs but not on low-stature dwarf shrubs, and this pattern was consistent between forest and tundra biomes. The bird predation pressure on defoliating insects increased with an increase in the levels of insect herbivory in forest habitats, but not in tundra habitats. Our findings indicate that birds preying on arthropods are unlikely to control insect herbivory in tundra ecosystems and shape the spatial patterns of plant losses to insects in Arctic ecosystems. We conclude that 'green world' hypothesis, as applied to birds, is not universal; further studies are needed to elucidate contributions of bird predation to variations in plant losses to insects at different temporal and spatial scales.

Compliance with ethical standards

Conflict of interest: The authors declare that they have no conflict of interest.

References

Adams JM, Zhang Y (2009) Is there more insect folivory in warmer temperate climates? A latitudinal comparison of insect folivory in eastern North America. J Ecol 97:933–940

Allen JA (1988) Frequency-dependent selection by predators. Philos Trans R Soc Lond B 319:485–503

Atlegrim O (1989) Exclusion of birds from bilberry stands: impact on insect larval density and damage to the bilberry. Oecologia 79:136–139

Barton KE, Koricheva J (2010) The ontogeny of plant defense and herbivory: characterizing general patterns using meta-analysis. Am Nat 175:481–493

Bianki VV, Kokhanov VD, Koryakin AS et al (1993) Birds of the Kola Peninsula and the White Sea region. Russ J Ornithol 2:491–586 **(in Russian)**

Björkman C, Berggren A, Bylund H (2011) Causes behind insect folivory patterns in latitudinal gradients. J Ecol 99:367–369

Bond AB, Kamil AC (2002) Visual predators select for crypticity and polymorphism in virtual prey. Nature 415:609–613

Brewer AM, Gaston KJ (2003) The geographical range structure of the holly leaf-miner. II Demographic rates. J Anim Ecol 72:82–93

Bruns H (1960) The economic importance of birds in forests. Bird Study 7:193–208

Champlin TB, Kilgo JC, Moorman CE (2009) Food abundance does not determine bird use of early-successional habitat. Ecology 90:1586–1594

Connor EF, Yoder JM, May JA (1999) Density-related predation by the Carolina chickadee, *Poecile carolinensis*, on the leaf-mining moth, *Cameraria hamadryadella* at three spatial scales. Oikos 87:105–112

Curio H (1976) The ethology of predation. Springer, Berlin

Galmán A, Abdala-Roberts L, Zhang S, Berny-Mier y Teran JC, Rasmann SO, Moreira X (2018) A global analysis of elevational gradients in leaf herbivory and its underlying drivers: effects of plant growth form, leaf habit and climatic correlates. J Ecol 106:413–421

Garibaldi LA, Kitzberger T, Noemí MT, Chaneton EJ (2010) Nutrient supply and bird predation additively control insect herbivory and tree growth in two contrasting forest habitats. Oikos 119:337–349

Giffard B, Corcket E, Barbaro L, Jactel H (2012) Bird predation enhances tree seedling resistance to insect herbivores in contrasting forest habitats. Oecologia 168:415–424

Gilyazova EV (1999) Changes in food composition of the European pied flycatcher, *Ficedula hypoleuca*, in relation to industrial pollution in the Kola Peninsula. Zapovednoe Delo [Nature Reserve Business, Moscow] 4:44–48 **(in Russian)**

González-Gómez PL, Estades CF, Simonetti JA (2006) Strengthened insectivory in a temperate fragmented forest. Oecologia 148:137–143

González-Salazar C, Martínez-Meyer E, López-Santiago G (2014) A hierarchical classification of trophic guilds for North American birds and mammals. Rev Mex Biodivers 85:931–941

Gripenberg S, Roslin T (2007) Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. Oikos 116:181–188

Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. Am Nat 94:421–425

Heads PA, Lawton JH (1983) Studies on the natural enemy complex of the holly leaf-miner: the effects of scale on the detection of aggregative responses and the implications for biological control. Oikos 40:267–276

Holmes RT, Robinson SK (1981) Tree species preferences of foraging insectivorous birds in a northern hardwoods forest. Oecologia 48:31–35

Holmes RT, Schultz JC (1988) Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Can J Zool 66:720–728

Howard LO, Fiske WF (1911) The importation into the United States of the parasites of the gipsy moth and the brown-tail moth: a report of progress, with some consideration of previous and concurrent efforts of this kind. US Bureau Entomol Bull 91:1–312

Howe A, Lövei GL, Nachman G (2009) Dummy caterpillars as a simple method to assess predation rates on invertebrates in a tropical agroecosystem. Entomol Exp Appl 131:325–329

Hunter MD (2016) The phytochemical landscape: linking trophic interactions and nutrient dynamics. Princeton University Press, Princeton

Hunter MD, Kozlov MV (2019) The relative strengths of rapid and delayed density dependence acting on a terrestrial herbivore change along a pollution gradient. J Anim Ecol 88:665–676

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732

Inozemtsev AA (1978) The role of insectivorous birds in forest ecosystems. Leningrad University Press, Leningrad (in Russian)

Itämies J, Ojanen M (1977) Autumn predation of *Parus major* and *P. montanus* upon two leaf-mining species of Lithocolletis (Lepidoptera, Lithocolletidae). Ann Zool Fenn 14:235–241

Johnson MTJ, Bertrand JA, Turcotte MM (2016) Precision and accuracy in quantifying herbivory. Ecol Entomol 41:112–121

Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago

Kenward MG, Roger JH (2009) An improved approximation to the precision of fixed effects from restricted maximum likelihood. Comput Stat Data Anal 53:2583–2595

Korňan M, Holmes RT, Recher HF, Adamík P, Kropil R (2013) Convergence in foraging guild structure of forest breeding bird assemblages across three continents is related to habitat structure and foraging opportunities. Community Ecol 14:89–100

Kozlov MV, Zvereva EL (2017) Background insect herbivory: impacts, patterns and methodology. In: Cánovas FM, Lüttge U, Matyssek R (eds) Progress in botany 79. Springer, Basel, pp 315–355

Kozlov MV, van Nieukerken EJ, Zverev V, Zvereva EL (2013) Abundance and diversity of birch-feeding leafminers along latitudinal gradients in Northern Europe. Ecography 36:1138–1149

Kozlov MV, Lanta V, Zverev V, Zvereva EL (2015a) Global patterns in background losses of woody plant foliage to insects. Glob Ecol Biogeogr 24:1126–1135

Kozlov MV, Filippov BY, Zubrij NA, Zverev V (2015b) Abrupt changes in invertebrate herbivory on woody plants at the forest-tundra ecotone. Polar Biol 38:967–974

Kozlov MV, Lanta V, Zverev V, Zvereva EL (2015c) Background losses of woody plant foliage to insects show variable relationships with plant functional traits across the globe. J Ecol 103:1519–1528

Kozlov MV, Lanta V, Zverev V, Rainio K, Kunavin MA, Zvereva EL (2017) Decreased losses of woody plant foliage to insects in large urban areas are explained by bird predation. Glob Chang Biol 23:4354–4364

Lim JY, Fine PVA, Mittelbach GG (2015) Assessing the latitudinal gradient in herbivory. Glob Ecol Biogeogr 24:1–7

Loiselle BA, Farji-Brener AG (2002) What's up? An experimental comparison of predation levels between canopy and understory in a tropical wet forest. Biotropica 34:327–330

Lövei GL, Ferrante M (2017) A review of the sentinel prey method as a way of quantifying invertebrate predation under field conditions. Insect Sci 24:528–542

Mac Nally R (1994) Habitat-specific guild structure of forest birds in south-eastern Australia: a regional scale perspective. J Anim Ecol 63:988–1001

Mäntylä E, Klemola T, Laaksonen T (2011) Birds help plants: a meta-analysis of top-down trophic cascades caused by avian predators. Oecologia 165:153–161

Martin TE (1987) Food as a limit on breeding birds: a life-history perspective. Annu Rev Ecol Syst 18:453–487

Nyffeler M, Şekercioğlu ÇH, Whelan CJ (2018) Insectivorous birds consume an estimated 400–500 million tons of prey annually. Sci Nat 105:47

Polis GA (1999) Why are parts of the world green? Multiple factors control productivity and the distribution of biomes. Oikos 86:3–15

Richards LA, Coley PD (2007) Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest. Oikos 116:31–40

Rosenberg MS, Adams DC, Gurevitch J (2000) MetaWin: Statistical software for meta-analysis, Version 2.0. Sinauer, Sunderland, MA

Roslin T, Hardwick B, Novotny V et al (2017) Higher predation risk for insect prey at low latitudes and elevations. Science 356:742–744

Ruiz-Guerra B, Nieves-Silva E, Guevara R (2017) The role of leaf traits and bird-mediated insect predation on patterns of herbivory in a semiarid environment in central Mexico. Bot Sci 95:189–201

SAS Institute (2009) SAS/Stat. User's guide, Version 9.2. SAS Institute, Cary, NY

Schwenk WS, Strong AM, Sillett TS (2010) Effects of bird predation on arthropod abundance and tree growth across an elevational gradient. J Avian Biol 41:367–377

Seifert CL, Lehner L, Adams M-O, Fiedler K (2015) Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica. J Trop Ecol 31:281–284

Singer MS, Farkas TE, Skorik C, Mooney KA (2012) Tri-trophic interactions at a community level: effects of host-plant species quality on bird predation of caterpillars. Am Nat 179:363–374

Sipura M (1999) Tritrophic interactions: willows, herbivorous insects and insectivorous birds. Oecologia 121:537–545

Strengbom J, Witzell J, Nordin A, Ericson L (2005) Do multitrophic interactions override N fertilization effects on *Operophtera* larvae? Oecologia 143:241–250

Stroup WW (2013) Generalized linear mixed models: modern concepts, methods and application. CRC Press, Boca Raton

Thiollay J-M (1988) Comparative foraging success of insectivorous birds in tropical and temperate forests: ecological implications. Oikos 53:17–30

Tinbergen L (1960) The natural control of insects in pine woods: I. Factors influencing the intensity of predation by songbirds. Archives Néerlandaises de Zoologie 13:265–343

Tvardikova K, Novotny V (2012) Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. J Trop Ecol 28:331–341

Wood EM, Pidgeon AM, Liu F, Mladenoff DJ (2012) Birds see the trees inside the forest: the potential impacts of changes in forest composition on songbirds during spring migration. Forest Ecol Manag 280:176–186

Zatsarinnyi IV, Timoshina YuA, Kosyakova AYu (2014) Composition of nestlting's food of Siberian tit, *Parus cinctus* in north-western part of Murmansk region. Russ Ornithol J 23:1594–1600 **(in Russian)**

Zverev V, Zvereva EL, Kozlov MV (2017) Ontogenetic changes in insect herbivory in birch (*Betula pubsecens*): the importance of plant apparency. Funct Ecol 31:2224–2232

Zvereva EL, Kozlov MV (2019) Biases in studies of spatial patterns in insect herbivory. Ecol Monogr 89:e01361

Zvereva EL, Castagneyrol B, Cornelissen T, Forsman A, Hernández-Agüero JA, Klemola T, Paolucci L, Polo V, Salinas N, Theron KJ, Xu G, Zverev V, Kozlov MV (2019) Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey. Ecol Evol 9:14273–14285