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Predation on Live and Artificial Insect Prey Shows Different Global Latitudinal Patterns

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Keywords: ants | arthropod predation | bird predation | forests | latitudinal pattern | live standardised prey | maggots | plasticine prey models | predation risk

ABSTRACT

Aim: Long-standing theory predicts that the intensity of biotic interactions increases from high to low latitudes. Studies addressing geographic variation in predation on insect prey have often relied on prey models, which lack many characteristics of live prey. Our goals were to explore global latitudinal patterns of predator attack rates on standardised live insect prey and to compare the patterns in predation on live insects with those on plasticine prey models.

Location: Global forested areas.

Time Period: 2021–2023.

Major Taxa: Arthropods, birds.

Methods: We measured predation rates in 43 forested locations distributed across five continents from 34.1° S to 69.5° N latitude. At each location, we exposed 20 sets of three bait types, one set per tree. Each set included three live fly larvae (maggots), three live fly puparia and three plasticine models of the puparia. We used glue rings to isolate half of the sets from non-flying predators.

Results: Arthropod attack rates on plasticine prey decreased linearly from low to high latitudes, whereas attack rates on maggots had a U shaped distribution, with the lowest predation rates at temperate latitudes and the highest rates at tropical and boreal latitudes. This difference emerged from intensive predator attacks on live maggots, but not on plasticine models, in boreal sites. Site-specific attack rates of arthropod predators on live and plasticine prey were not correlated. In contrast, bird attack rates on live maggots and plasticine models were positively correlated, but did not show significant latitudinal changes.

Main Conclusions: Latitudinal patterns in predation differ between major groups of predators and between types of prey. Poleward decreases in both arthropod and combined arthropod and bird predation on plasticine models do not mirror patterns of predation on our live prey, the latter likely reflecting real patterns of predation risk better than do patterns of attack on artificial prey.

1 | Introduction

The Latitudinal Biotic Interaction Hypothesis (LBIH) postulates that the strength of biotic interactions increases from high to low latitudes (Schemske et al. 2009). This hypothesis has generally been supported for herbivory and carnivory (McKinnon et al. 2010; Roslin et al. 2017; Hargreaves et al. 2019; Zvereva and Kozlov 2021a). However, the outcomes of individual studies are highly variable, with some providing partial or no support for the LBIH (Moles et al. 2011; Kozlov et al. 2015; Mottl et al. 2020). Variation in the outcomes of individual studies on global predation patterns can be driven by different characteristics of both predators and prey (Roslin et al. 2017; Zvereva et al. 2019; Zvereva and Kozlov 2021a; Hargreaves et al. 2019). For example, a poleward decrease in predation by ectothermic but not endothermic predators has been observed (Roslin et al. 2017; Zvereva et al. 2019; Zvereva and Kozlov 2021a) and latitudinal patterns in predation on model prey vary with prey colour (Zvereva et al. 2019). As a result, the generality of the LBIH is debated, and a comprehensive understanding of latitudinal patterns in predation has yet to be fully established.

Another potential source of variation in reported latitudinal trends in the intensity of biotic interactions is research methods (Anstett et al. 2016; Zvereva and Kozlov 2021a). The use of standardised prey can help enhance consistency in methods (Roslin et al. 2017). Consequently, artificial prey models are increasingly employed in studies of geographic patterns in predation. For example, researchers frequently use artificial bird nests (Söderström 1999; McKinnon et al. 2010) or caterpillar-shaped plasticine models (Lövei and Ferrante 2017; Roslin et al. 2017; Zvereva et al. 2019; Zverev, Zvereva, and Kozlov 2020; Zvereva, Zverev, and Kozlov 2020). However, artificial insect models do not provide the entire complex of cues used by predators in prey search and selection (Lövei and Ferrante 2017). Moreover, artificial prey are not a reward to predators, thus decreasing the probability of repeated attacks. Therefore, predation rates measured on models are generally lower than those measured on live prey (Lövei and Ferrante 2017), although exceptions have been reported from the tropics (Remmel, Davidson, and Tammaru 2011). Direct comparisons of spatial patterns in predation on live and artificial prey are rare (Molleman, Remmel, and Sam 2016; Zvereva, Zverev, and Kozlov 2020; Rodriguez-Campbell et al. 2024). Such comparisons are necessary because artificial prey models can be used to standardise measurements of predation rates only if they accurately reflect patterns of predation on live prey. Assessing whether live and artificial prey capture the same trends in predation strength across latitudes would provide insights into the viability of artificial prey as a reliable means of quantifying geographic patterns of predation.

We suggest that use of live prey has the potential to illuminate patterns different from those obtained with artificial prey. Live standardised prey are likely to better mirror real predation patterns than artificial prey, because live prey have a greater number of cues for predators, in particular movements and chemical cues, than plasticine prey. However, natural prey usually have anti-predator adaptations, including crypsis and defences (Ruxton et al. 2018), which may reduce predation risk, and these adaptations vary considerably among prey species and locations. Use of live prey with no obvious antipredator adaptations is therefore more suitable than other natural prey for comparisons of latitudinal patterns in predation risk between plasticine and live prey. Fly (Diptera) larvae (maggots) and their puparia, which live hidden within substrates, such as decaying organic matter, have weak protection against enemies (Witz 1990) but still provide cues to predators. Maggots and mealworms, which are reared by multiple companies across the world, sometimes have been used to measure local predation pressure (Drozdová, Šipoš, and Drozd 2013; Zvereva and Kozlov 2023; Nimalrathna et al. 2023), but few attempts have been made to use live standardised prey to explore geographic variation in predation (but see Jeanne 1979; Rodriguez-Campbell et al. 2024).

The goal of this study was to test whether latitudinal patterns in predation on plasticine models of insects and on live insects are same. We measured predator attack rates on standardised live prey and plasticine prey models in multiple locations around the globe, with the same protocol at each location. We also tested whether estimates of predation rates on live and artificial prey differed between arthropod and vertebrate (bird) predators.

2 | Materials and Methods

2.1 | Study Design

The lead author first invited researchers with whom she previously collaborated, and others who were recommended by these researchers, to take part in this study. We did our best to achieve even distribution among continents and latitudes. After several spatial gaps were revealed, researchers working in underrepresented regions were invited on the basis of topics of their publications. The protocol (Text S1 in Supporting Information), recording form (Table S1), plasticine and non-drying glue (specified below) were mailed to all collaborators.

We measured attack rates by predators in forested sites at 43 locations in 23 countries in five continents from 34.1° S to 69.5° N latitude and from 4 to 1400 m elevation (median value 200 m a.s.l.) across three geographic zones—tropical, temperate and boreal (Figure 1a)—from 2 July 2021 through 12 July 2023 (Table S2) with the method designed by Zvereva and Kozlov (2023). Collaborators were responsible for selecting a forested site that was typical of their geographic region and with minimal human disturbance at the elevations as close as possible to sea level. In temperate and boreal zones, the experiments were conducted during the breeding season of local birds, spring and early summer, whereas in the tropics, where the breeding season is year round, field work did not take place at a set time of year.

We used three kinds of prey at each site: live fly larvae (maggots; white, 10–13 mm long), live fly puparia (brown, 7–8 mm long) and plasticine models of the puparia (brown, 7–8 mm long). We used blowfly (Calliphoridae) maggots and puparia in the majority of sites, but in eight sites (Table S2), we used black soldier fly (*Hermetia illucens* L., Stratiomyidae), and in one site, we used *Peckia* sp. (Sarcophagidae) because blowfly larvae were not available. Larvae of black soldier flies used in our experiments had lengths similar to those of blowfly larvae but were slightly

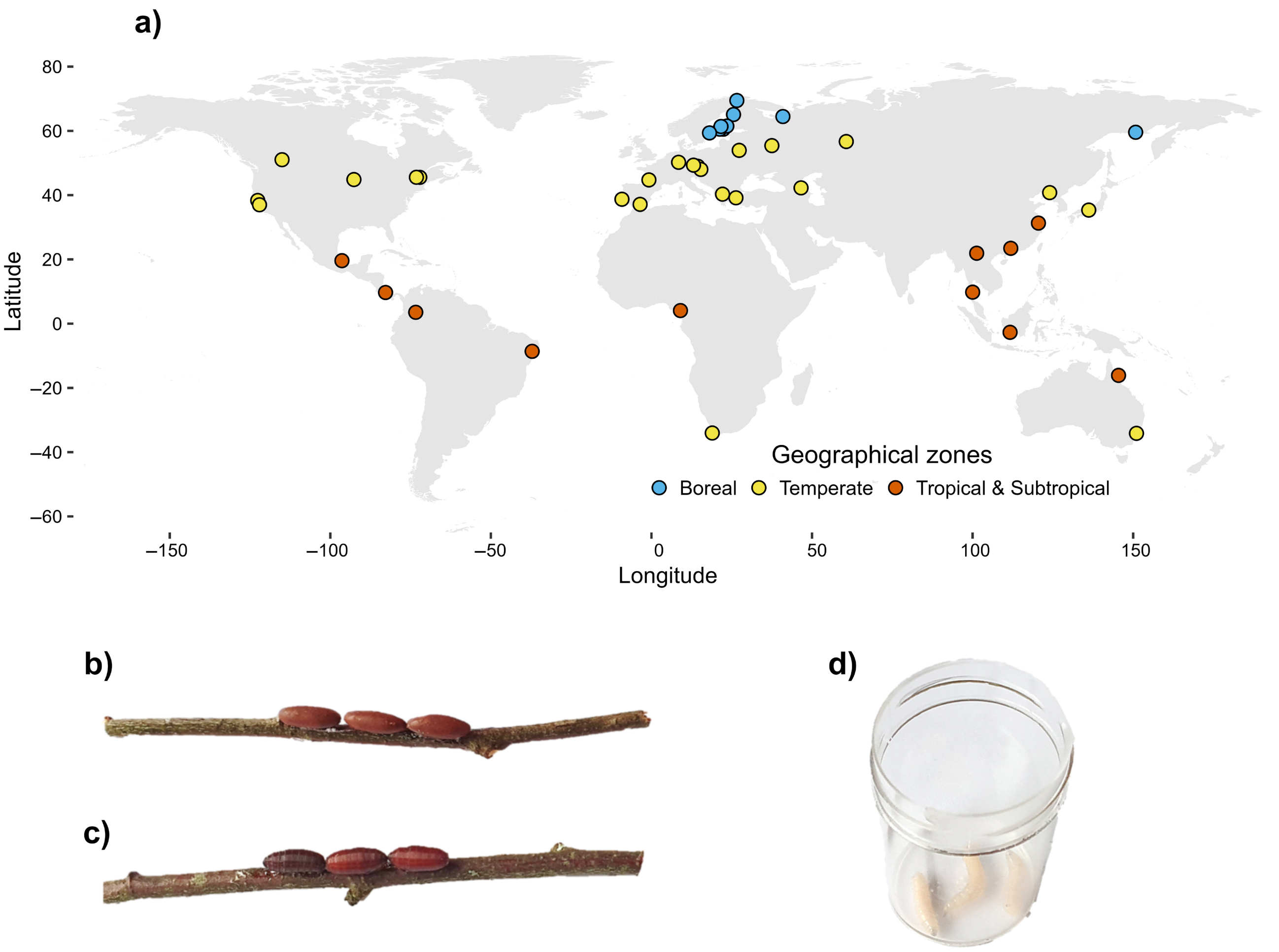

FIGURE 1 | Locations of study sites (a) and a set of baits used in the study: Plasticine models of puparia (b), live puparia (c) and vial with maggots (d). For detailed information on each site, refer to Table S2.

darker and sparsely covered with thin hairs. An experiment conducted in Finland that simultaneously exposed maggots of blowflies and black soldier flies on 10 trees revealed no differences in predation rates (Wilcoxon signed rank test: $S=6$, $n=10$ trees, $p=0.19$, unpublished data, ELZ). Overall, predation on live prey (maggots and puparia) did not differ between experiments that used blowflies and black soldier flies ($F_{1,38}=0.60$, $p=0.44$), and therefore we pooled data from experiments with blowflies and black soldier flies.

Each collaborator obtained live maggots in their last instar from producers of fish baits or animal food; two collaborators reared maggots from eggs laid by local flies on meat. Rearing and storage temperatures were manipulated to obtain both maggots and puparia by the start of the experiments. All collaborators used the same plasticine (produced by "Luch", Yaroslavl, Russia), advertised as non-toxic and unscented. We mixed red and black plasticine to obtain a brown colour similar to that of puparia; we moulded plasticine in the shape and size of puparia. We glued three individual puparia and three plasticine models of puparia in a line along a stick cut from a thin branch (Figure 1b,c and photos in Text S1).

Ten pairs (blocks) of young (2–3 m tall) individuals of the most abundant woody species were selected at each site (20 trees per site). If only large trees (over 5 m tall) were available at the site, then two accessible branches on 10 trees were considered as the ten blocks. In each block, we isolated one tree or branch from non-flying arthropod predators by encircling the base with a ring of non-drying glue (hereafter 'non-flying predator exclusion'). We removed all arthropods from these isolated trees or branches and prevented the intrusion of non-flying arthropod predators (with the potential exception of spiders) by removing branches touching neighbouring trees. The second tree or branch in each block remained accessible to non-flying arthropod predators and served as the control for arthropod predation. The distance between treatments within a block ranged from 0.5 to 3 m, and the distance between nearest blocks was at least 10 m.

We placed three types of prey items on each of the 20 trees or branches: an open transparent plastic vial (40–50 mm in height and 30–40 mm in diameter) containing three live maggots, one stick with three puparia and another stick with three plasticine models of puparia (Figure 1b–d; Text S1). We placed a small stick in each vial to ease the movement of predatory arthropods (we previously verified that the maggots were incapable of climbing up the stick and dry walls of the vial: Zvereva and Kozlov 2023). For more details, see the protocol (Text S1 in Supporting Information).

We chose a period for prey exposure when there was no anticipated rainfall, with a particular focus on the initial 24 h. However, maggot baits from two sites were omitted from data analysis due to unforeseen rain that resulted in maggots either drowning or escaping from vials when the walls of the vials became wet. After 24 h, on both treatment and control branches, we recorded (i) the number of maggots that had disappeared from each vial, (ii) the number of dead maggots in each vial, (iii) the number of damaged puparia and (iv) the presence of attack marks by arthropods, birds and other predators on each plasticine model. Three to seven days after the start of the experiment, we again recorded (iii) and (iv). Here we used the cumulative number of attacked puparia and their plasticine models from the beginning of the experiment. The second record was missed in one location (Dagestan, Russia) due to logistical obstacles. Each collaborator distinguished bird and arthropod attacks on plasticine models according to Low et al. (2014). Problematic attack marks on plasticine models and live puparia were photographed and images emailed to E.L.Z. for identification. Collaborators also recorded their observations of attacks of predators on the baits, and collected ants on tree trunks and branches for 15 min for further identification by local experts or P.K.

We estimated attack rates on maggots from the first record only (after 24 h) because in most sites at least one rain occurred after the first exposure period or many maggots pupated or died due to desiccation. Maggots in vials were not attacked by birds (Zvereva and Kozlov 2023), possibly because birds are frightened by an unknown object (glossy vial) or vials were too deep for birds to reach maggots. We estimated bird predation rates on live puparia and plasticine models from both the first and second records. Puparia glued to the stick were seldom attacked by arthropod predators (Remmel and Tammaru 2009; Zvereva and Kozlov 2023). Therefore, we estimated arthropod predation on live prey from maggots and bird predation on live prey from puparia (Figure S1). Only ten attack marks on plasticine models (of 1220) were attributed to vertebrate predators other than birds, and therefore only bird predation was included in the analysis of vertebrate predation.

2.2 | Data Analysis

Although our data are binomial, the binomial model did not converge because the data were zero-inflated. Therefore, following Zvereva and Kozlov (2023), we calculated daily predation rates by dividing the number of prey that disappeared from each vial (maggots) or were attacked (puparia and models) by the duration of exposure from the start of the experiments (in days); we expressed predation rates as the percentage of prey items attacked. We calculated attack rates on models separately for bird and arthropod predators. Dead maggots in a vial were also considered as preyed on, as some arthropods (e.g. spiders and true bugs) consume prey on site without carrying it away (Table S2).

We used a linear mixed model (SAS GLIMMIX procedure, type III tests; SAS Institute 2009) to analyse daily predation rates, which we square root transformed to achieve normality of residuals. We considered latitude as a covariate and treatment (non-flying arthropods excluded or not excluded) and the interaction between latitude and treatment as fixed effects. We included a random effect for sites nested within geographic zones (defined below) and blocks (i.e., pairs of trees or branches) nested within sites. We used this analysis to test the hypothesis that predation rates increase with decreasing latitude.

We used Wilcoxon signed rank test (SAS UNIVARIATE procedure; SAS Institute 2009) to compare site-specific values of arthropod and bird predation rates on both live and plasticine prey on control trees. We explored the relationships between predation rates on live and plasticine prey by calculating Pearson linear correlation coefficients of square-root transformed values (SAS CORR procedure; SAS Institute 2009). Visual examination of latitudinal patterns hinted that they could be non-linear for some prey types. We therefore compared the residual variation of the paired linear and quadratic regression models of arthropod predation rates on both types of prey by calculating the Akaike information criterion corrected for small sample size (AICc; graphpad.com/quickcalcs/AIC1.cfm) and used ΔAICc = 2 as an evidence of a difference in the models.

To further investigate the U-shaped pattern in predation on maggots (see below), we assigned sites to one of three geographic zones on the basis of absolute latitude: tropical (which included one subtropical site; below 31° N/S), temperate (31°–59.5°) and boreal (above 59.5° N), and we replaced continuous latitude (covariate) in a mixed model with geographic zone (fixed effect). We adjusted the standard errors and denominator degrees of freedom for the fixed effects following Kenward and Roger (2009), used a likelihood ratio test (Stroup 2013) for random effects and compared estimated marginal means with *t*-tests (SAS Institute 2009).

3 | Results

3.1 | Arthropod Predation

Attack rates by arthropod predators on plasticine models significantly decreased towards the poles (Figure 2a; $F_{1,41.4} = 7.11$, $p = 0.01$). In contrast, arthropod attack rates on live maggots were not linearly related to latitude ($F_{1,39.1} = 2.00$, $p = 0.17$) but instead were best described by a quadratic (U-shaped) function (Figure 2b) (difference in AICc is 5.12). Attack rates on live maggots were not correlated with attack rates on plasticine models across locations ($r = 0.27$, $n = 41$ locations, $p = 0.09$). This lack of correlation resulted from intensive arthropod predation on maggots in boreal forests, which was as high as in tropical forests and significantly higher than in temperate forests (Figure 3b). Predation on plasticine models in both temperate and boreal forests was lower than in tropical forests (Figure 3a).

Predation rates by arthropods on maggots and plasticine models of puparia varied significantly among geographic zones and among sites within each zone (Table 1). Across all sites, arthropod attack rates on control trees or branches were 5.5 times greater on maggots than on plasticine models of puparia (Figure 4). However, the magnitude of the difference between arthropod predation on maggots and plasticine models varied among geographic zones: predation on maggots was five and three times greater than predation on models on control trees

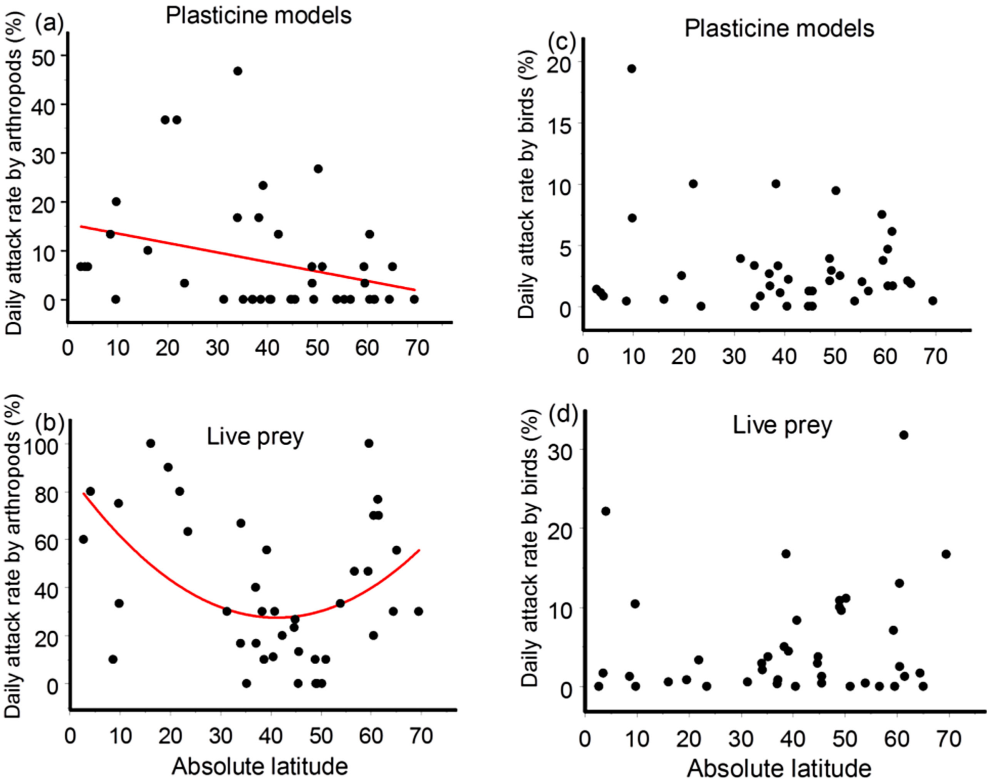

FIGURE 2 | Relationship between the observed site-specific daily attack rates by arthropod (a, b) and bird (c, d) predators on control plants (based on the first and the second record, respectively) and latitude of study sites on plasticine models (a, c) and live maggots (b, d). Red lines show best-fit approximations: (a) linear ($R^2 = 0.114$, $p = 0.03$), (b) quadratic ($R^2 = 0.215$, $p = 0.01$), (c) no significant effect ($R^2 = 0.004$, $p = 0.69$), (d) no significant effect ($R^2 = 0.050$, $p = 0.15$). All analyses are based on square-root transformed values.

in tropical and temperate forests, respectively, and 16 times greater in boreal forests (Figure 3a,b).

Excluding non-flying arthropod predators significantly decreased predation on maggots in all geographic zones (Figure 3b). In contrast, this treatment reduced predation on models in tropical and temperate forests, but not in boreal forests (Figure 3a).

We observed several groups of arthropod predators attacking maggots in vials. Ants were seen attacking maggots at 20 of 21 sites where predator attacks were observed. The next most commonly observed arthropod predators of maggots were spiders (two sites) (Table S2). We observed attacks by ants on live puparia at eight sites, significantly fewer than on maggots ($\chi^2 = 8.09$, $p = 0.01$). No arthropod predators were seen attacking plasticine models (Table S2).

3.2 | Bird Predation

The effect of latitude on predation by birds on either live or model puparia was not significant (Figure 2c,d; $F_{1,40.6} = 0.89$, $p = 0.35$ and $F_{1,39.2} = 0.08$, $p = 0.77$, respectively). Similarly, bird predation did not vary among geographic zones, although among-site variation within zones was highly significant (Table 2). Excluding non-flying arthropods did not affect bird attack rates on either live or artificial prey (Table 2). The correlation between bird attack rates on live puparia and their models across locations approached the conventional level of statistical significance ($r = 0.29$, $n = 42$ locations, $p = 0.06$).

Across all sites, bird attack rates on live puparia were 1.4-fold higher compared to those on their plasticine models (Figure 4). These differences were significant in both temperate and boreal forests, but not in tropical forests (Figure 5).

3.3 | Total Predation

Overall, bird attack rates were significantly lower than arthropod attack rates on both plasticine models and live prey (Figure 4), although on plasticine models these differences were only marginally significant ($p = 0.06$). Consistently, the total attack rate (arthropods and birds combined; based on the first record on control branches) on plasticine models decreased linearly with increasing latitude ($R^2 = 0.17$, $F_{1,41} = 8.25$, $p = 0.01$), whereas the total attack rate on live prey was better described by a quadratic ($R^2 = 0.14$, $F_{2,38} = 3.17$, $p = 0.05$) than by a linear ($R^2 = 0.01$, $F_{2,38} = 0.43$, $p = 0.52$) model (difference in AICc is 3.14), consistent with the patterns of arthropod predation (Figure S1).

4 | Discussion

4.1 | Latitudinal Gradient in Predation on Plasticine Prey is Not Found for Live Prey

To our knowledge, this is the first study to explore global latitudinal pattern in predation rate on standardised live insect prey (maggots) across forests in all climate zones and continents

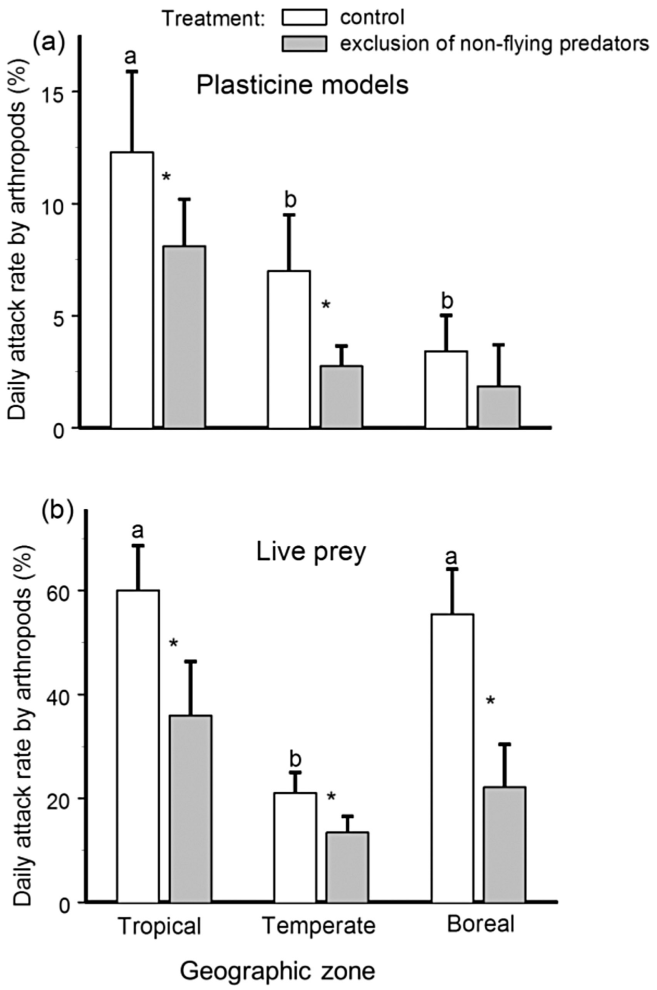

FIGURE 3 | Attack rates by arthropod predators in tropical (11 sites), temperate (23 sites) and boreal (9 sites) forests on plants with excluded non-flying predators and control plants on plasticine models (a) and live maggots (b) during first day of exposure. Values are observed means ± SE. Bars marked with different letters show significant differences between geographic zones for control plants; asterisks indicate significant differences between predation on control plants and plants with non-flying predators excluded (mixed model ANOVA, *t*-test).

and to compare predation on live prey and plasticine models. We found that arthropod predation on plasticine models declined monotonically with increasing latitude. This result is consistent with those from previous studies that used plasticine models (Roslin et al. 2017; Zvereva et al. 2019), which have been interpreted as strong support for the Latitudinal Biotic Interaction Hypothesis (LBIH). In contrast, arthropod predation on live prey in our study was best described by a U-shaped function, a result consistent with LBIH predictions for tropical and temperate latitudes only. The mismatch in latitudinal patterns of predation on live and plasticine prey resulted from intense arthropod predation on maggots in boreal forests, whereas predation on plasticine models in these forests was extremely low.

In our study, high predation rates in tropical locations were primarily caused by non-flying arthropods, especially ants. This finding is consistent with numerous other studies conducted in the tropics (Jeanne 1979; Tvardikova and Novotny 2012; Sam, Remmel, and Molleman 2015; Camacho and Avilés 2019; Nimalrathna et al. 2023). Additionally, we demonstrated that attack rates by ants on live maggots in boreal forests were as high as those in tropical forests. In Scandinavian boreal forests, daily predation rates by ants on live prey may reach 60% (Zvereva and Kozlov 2023) or even 100% (Figure 2b), underscoring the significant ecological role of wood ants (*Formica* spp.) as predators of herbivorous insects in boreal forests (Punttila, Niemelä, and Karhu 2004; Domisch et al. 2009; Maňák et al. 2013). In contrast, *F. polyctena* in these forests did not attack plasticine prey in a behavioural experiment and consequently did not leave marks on the surface of the model (Zvereva and Kozlov 2023).

The differences in ant attack rates on plasticine models between tropical and boreal forests may result from the specificity of feeding strategies of wood ants. The wood ants that dominate our boreal sites (Table S2) require protein-rich food (prey) for feeding their progeny and queen (Sundström 1993; Lenoir 2002) and therefore need to carry prey to their nest. Partly for that reason, ants may ignore plasticine models attached to the branch. Ants in tropical forests are more diverse than in boreal forests (Table S2) and include specialised predators that also consume prey themselves (Lach, Parr, and Abbott 2009).

The observed differences in arthropod attack rates on plasticine models between tropical and boreal forests may also result from differences in nutritional requirements of ants inhabiting these forests. Tropical ants select oil baits as frequently as sugar baits (Peters et al. 2014; Lasmar et al. 2021), whereas ants dominating temperate and boreal forests (mostly *Formica* spp.) generally ignore oil baits (Spotti et al. 2015; Guariento, Wanek, and Fiedler 2021; Bezděčková et al. 2024). The plasticine we used contains oils, and therefore greater demand of tropical ants for oil may explain their higher attack rates on plasticine models in tropical forests relative to boreal forests.

The latitudinal pattern of overall predation is driven by arthropod predators (Roslin et al. 2017; this study). Therefore, our finding that the latitudinal pattern in arthropod predation on live maggots has two peaks, one in tropical and one in boreal forests, challenges the concept of linear decrease in overall predation on arboreal insects with increasing latitude, which was found on plasticine models only (Roslin et al. 2017; Zvereva et al. 2019).

4.2 | No Latitudinal Changes in Predation by Birds

Similar to arthropod predation, predation by birds on live puparia was generally higher than on plasticine models of puparia. Avoidance of plasticine models cannot be explained by learning associated with no-reward prey because we recorded predation during the first 24 h of exposure; instead, avoidance likely indicates that birds to some degree can distinguish edible and inedible objects without attacking them (Zvereva and Kozlov 2023).

TABLE 1 | Effects of geographic zone (tropical, temperate and boreal), treatment (exclusion of non-flying predators and control) and study site on daily arthropod attack rates on live maggots and plasticine models (based on the first record; attack rates square-root transformed; SAS GLIMMIX procedure, type III tests).

Prey	Effect	Source of variation	Degrees of freedom		Statistics	Value	*p*
Live	Fixed	Zone	2	38.1	*F*	7.82	0.001
		Treatment	1	401.5	*F*	76.39	<0.0001
		Zone × Treatment	2	401.5	*F*	11.56	<0.0001
	Random	Site (Zone)	1	—	χ^2	131.28	<0.0001
		Block (Site)	1	—	χ^2	3.21	0.07
Model	Fixed	Zone	2	40.2	*F*	4.09	0.02
		Treatment	1	423.1	*F*	6.64	0.01
		Zone × Treatment	2	423.0	*F*	0.14	0.87
	Random	Site (Zone)	1	—	χ^2	59.67	<0.0001
		Block (Site)	1	—	χ^2	1.41	0.24

We found no effect of latitude on predation by birds on either live puparia or plasticine models. This pattern is consistent with those reported by Roslin et al. (2017) for plasticine models and by Lövei and Ferrante (2017) for different kinds of prey. However, we found significant geographic variation in bird predation that was unrelated to latitude. This geographic variation estimated on plasticine models, correlates with variation estimated on live prey, suggesting that this variation can be studied with models of prey. The striking difference between bird and arthropod predation on models may result from the greater importance of visual cues for birds than for arthropods (Ruxton et al. 2018). Models can mimic shape and colour of natural prey, but not chemical characteristics of prey, which are critical for arthropod predators.

4.3 | Importance of High Latitudes for Development of Macroecological Theories

The great majority of studies on which the LBIH is based (reviewed by Schemske et al. 2009) are limited to comparisons between tropical and temperate zones (e.g. Jeanne 1979; Coley and Barone 1996). These previous studies and our current study detected considerably greater intensity of biotic interactions in tropical than temperate zones, supporting the prediction of the LBIH that the strength of biotic interactions decreases towards the poles. Similarly, predation rates on insects, especially by arthropods, decline towards the poles at the forest-tundra ecotone (Zverev, Zvereva, and Kozlov 2020). Ant abundance in tundra is extremely low (Schultheiss et al. 2022), which partly explains the strong poleward decrease in arthropod predation on plasticine models reported by Roslin et al. (2017) and on seeds by Hargreaves et al. (2019), both of which included tundra sites. Our discovery of high ant predation on live insect prey in boreal forests, resulting in two peaks in the latitudinal gradient in predation risk for insects, indicates that including high-latitude sites in analyses of global ecological patterns may lead to modifications of existing theories or refinements in the theories' scope.

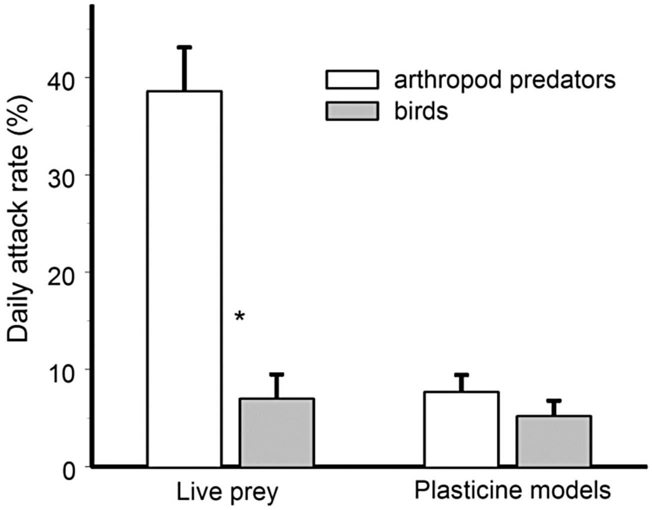

FIGURE 4 | Overall daily attack rates by arthropod predators and birds on live prey (maggots for arthropods and puparia for birds) and plasticine models (based on first record) across all study sites. Values are site-specific means ± SE. An asterisk indicates significant ($p < 0.05$) differences between values (Wilcoxon signed rank test).

4.4 | Biases in Predation Studies

Our study is consistent with the inference that predator attack rates on artificial prey are generally lower than those on live prey (Lövei and Ferrante 2017). While it was assumed that this bias is consistent across space and time, recent study shows that it varies with season (Zvereva and Kozlov 2023). Our current study also reveals that the bias in estimation of predation risk from use of plasticine models is stronger in boreal forests than in tropical and temperate forests (Figure 3). The spatial and temporal variation in biases may affect some areas of research. For example, data from Roslin et al. (2017) that demonstrated a strong decrease in predation on plasticine models with increasing latitude were used to predict the distribution of predation pressure under future climate scenarios

TABLE 2 | Effects of geographic zone (tropical, temperate and boreal), treatment (exclusion of non-flying predators and control) and study site on daily bird attack rates on live fly puparia and plasticine models (based on the second record; attack rates are square-root transformed; SAS GLIMMIX procedure, type III tests).

Prey	Effect	Source of variation	Degrees of freedom		Statistics	Value	*p*
Live	Fixed	Zone	2	39.4	*F*	1.03	0.37
		Treatment	1	407.0	*F*	0.36	0.55
		Zone × Treatment	2	406.9	*F*	2.75	0.07
	Random	Site (Zone)	1	—	χ^2	201.33	<0.0001
		Block (Site)	1	—	χ^2	12.67	0.0004
Model	Fixed	Zone	2	38.1	*F*	0.88	0.42
		Treatment	1	411.5	*F*	0.44	0.51
		Zone × Treatment	2	411.4	*F*	2.28	0.10
	Random	Site (Zone)	1	—	χ^2	64.87	<0.0001
		Block (Site)	1	—	χ^2	3.51	0.06

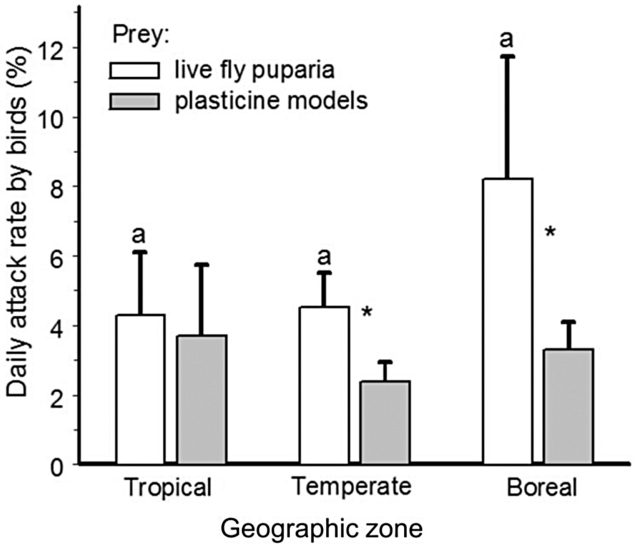

FIGURE 5 | Attack rates by birds in tropical (11 sites), temperate (23 sites) and boreal (9 sites) zones on live fly puparia and plasticine models of puparia (based on second record). Values are observed means ± SE. Bars marked with different letters indicate significant differences between zones; asterisks indicate significant difference in predation on different prey types (mixed model ANOVA, *t*-test).

(Romero et al. 2018). Our finding of high predation risk for insects in high latitude forests that we estimated from live prey challenges these predictions.

The possibility of distinguishing groups of predators by their attack marks is often considered to be one of the advantages of plasticine models (Low et al. 2014; Rößler, Pröhl, and Lötters 2018). However, some arthropod predators avoid plasticine prey, leaving no marks at all (Greenop et al. 2019; Khan and Joseph 2021; Zvereva and Kozlov 2023; Yan et al. 2024), which can bias conclusions about the relative effectiveness of different members of the predator community.

Biases from use of plasticine models to estimate arthropod predation are especially important, because arthropods govern geographic patterns in predation (Roslin et al. 2017; Hargreaves et al. 2019; this study). We suggest that standardised live prey, such as maggots or mealworms, have considerable advantages over plasticine models in studies measuring the rates of arthropod predation. First, live insects provide more cues used by predators to search for prey and are therefore attractive to a wider range of predators than plasticine models. Second, use of live prey yields higher values of predation rates than use of plasticine models (Figure 4), which facilitates accurate measurements of predation rates after a one-day exposure. Third, recording missing and dead prey is easier than detection and accurate identification of attack marks on plasticine, which requires some experience (Valdés-Correcher et al. 2022). Fourth, the likelihood of detecting arthropod predation on live prey is not affected by temperature, whereas the visibility of attack marks on plasticine significantly declines at low temperatures (Muchula, Xie, and Gurr 2019). This temperature-related bias could be particularly important in global studies.

Every method is likely to have some potential biases, and our study is no exception. First, to estimate arthropod predation, we used maggots as live prey and plasticine puparia as artificial models. We made this decision because it is not possible to offer live maggots in the same way as puparia without killing them. Selection of a single tree species in each site can also impose some bias, because predation rates may differ between tree species (Singer et al. 2012; Hernández-Agüero et al. 2020; Zvereva and Kozlov 2021b). However, because we used the most abundant tree species in each site, this bias in estimation of site-specific values should not be considerable.

We assessed predation in temperate and boreal zones during the breeding season of local birds. This timing avoided bias from predation by juvenile birds, which are present in the population for only a short period but differ from adult birds in selectivity of prey choice (Mappes et al. 2014; Zvereva and Kozlov 2023).

However, this method was not followed in the tropical zone, where different bird species breed at different times of the year or constantly during the year (Stouffer, Johnson, and Bierregaard Jr. 2013). The presence of juveniles in bird populations could cause higher bird predation on plasticine models in tropics, but we did not observe this increase. Therefore, seasonal differences in the timing of the experiment likely did not influence our conclusions.

Our study also suffers geographic bias due to our failure to find any collaborator in the boreal zone in North America. The lack of data from this region could potentially affect the generality of our conclusion about geographic patterns in arthropod predation, as some studies conducted in the Americas showed a monotonic decrease in arthropod predation with increasing latitude, at least for predation on bird nests (McKinnon et al. 2010) and seeds (Hargreaves et al. 2019). Whether *Formica* wood ants in North American boreal forests could play the same role that they do in Scandanavia is not known (Jurgensen, Storer, and Risch 2005).

Despite the limitations listed above, we conclude that the global poleward decrease in predation on plasticine models does not mirror the pattern that we report here for standardised live prey (maggots). Our study underscores the pivotal role of live prey studies in accurately depicting predation patterns across latitudes.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data used in this work are archived in Figshare and available at https://doi.org/10.6084/m9.figshare.26340373.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.