







# The effects of human population density on trophic interactions are contingent upon latitude

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## Abstract

**Aim:** Global-scale studies are necessary to draw general conclusions on how trophic interactions vary with urbanization and to explore how the effects of urbanization change along latitudinal gradients. We predict that the intensity of trophic interactions decreases in response to urbanization (quantified by human population density). Since trophic interactions are more intense at lower latitudes, we also expect major impacts of urbanization at higher latitudes, where base levels are essentially lower.

**Location:** Global (881 study sites).

**Time period:** 2000–2021.

**Major taxa studied:** Birds, arthropods and woody plants.

**Methods:** We compiled global data on insect herbivory and bird predation from studies that employed similar methods and fitted generalized linear mixed models to test how these trophic interactions vary with human population density, latitude and their interactions.

**Results:** The intensity of herbivory and predation decreased with an increase in human population density at lower latitudes. Surprisingly, it remained unaffected at intermediate latitudes and even increased at higher latitudes.

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**Main conclusions:** The observed patterns may be attributed to local climate changes in urban areas, such as the Urban Heat Island effect, which disrupts thermal stability in the tropics while increasing niche availability at polar latitudes.

**KEYWORDS**

bird predation, climate change, heat island effect, insect herbivory, latitude, macroecology, urbanization

## 1 | INTRODUCTION

Among human activities causing habitat loss, urban development produces some of the most significant local extinction rates (McKinney, 2002). Currently, 54% of the world's population live in cities (with  $\geq 300,000$  inhabitants), and this percentage is expected to increase to 70% by 2050 (United Nations, 2018). Highly populated areas frequently experience air and water pollution issues, leading to significant changes in ecosystems, land use, biogeochemical cycles and climate (Bai et al., 2017). These impacts contribute to a decline in the abundance and diversity of various taxa, including bats (Russo & Ancillotto, 2015), birds (Gagné & Fahrig, 2011; Planillo et al., 2021), fungi (Abrego et al., 2020), beetles (Gagné & Fahrig, 2011), bees (Fortel et al., 2014) and other insects (Planillo et al., 2021).

Shifts in species composition, abundance and diversity of biota driven by urbanization can also have significant effects on trophic interactions. These interactions are particularly relevant for biological communities and critical ecosystem services, such as nutrient cycling (DeAngelis, 2012), pest control (Whelan et al., 2008), adaptation to the effects of climate change, or human health (Sirakaya et al., 2018). According to the 'increasing disturbance' hypothesis (Eötvös et al., 2018), urbanization decreases the intensity of trophic interactions, such as herbivory or predation. Supporting evidence for this hypothesis has been found in Europe (Kozlov et al., 2017; Moreira et al., 2019) and the USA (Meineke et al., 2019).

A recent review article concludes that urbanization could affect both adaptive and non-adaptive evolution of herbivorous arthropods and their host plants in urban environments, altering plant-herbivore interactions. However, changes in the abundance of native species appear to be species-specific, with no general consensus on their effects (Miles et al., 2019). For predation, evidence supporting the 'increasing disturbance' hypothesis includes the reduction in predator abundance in response to urbanization in southern England (Rocha & Fellowes, 2018), as well as decreased predation observed in Finland (Jokimäki & Huhta, 2000), Denmark (Ferrante et al., 2014), Madagascar (Schwab et al., 2020), North America (Gering & Blair, 1999; Thorington & Bowman, 2003) and across all of Europe (Eötvös et al., 2018).

Despite widespread support for the 'increasing disturbance' hypothesis, some studies have also reported a positive effect of urbanization on herbivory in different parts of the world, including Brazil (Cuevas-Reyes et al., 2013; Rivkin & de Andrade, 2023), Australia (Christie & Hochuli, 2005) and the USA (Cregg & Dix, 2001; Dale &

Frank, 2017). Likewise, predation by birds and arthropods has been shown to increase across disturbance gradients in the Philippines (Posa et al., 2007) and in Europe (Kozlov et al., 2017). Different hypotheses might explain these contrasting results. Firstly, the 'predator relaxation/safe habitat' hypothesis (Noske, 1998) proposes that there are fewer predators in disturbed areas, resulting in less prey mortality and, consequently, an increase in herbivory. This, in turn, reduces the need for vigilance behaviour, allowing an increase in other activities such as feeding or reproduction. Similarly, the 'natural enemy release' hypothesis (Keane & Crawley, 2002) proposes that urban areas with less complex vegetation may support fewer natural enemies. This decrease in the biological control of pests allows herbivore species to proliferate (Dale & Frank, 2017; Meineke et al., 2014). Additionally, the 'plant stress' hypothesis proposes that herbivore species could proliferate in urban areas due to a reduction in defence investment in plants caused by water stress, elevated temperatures and pollution (White, 1969). Simultaneously, the 'plant vigour' hypothesis explains the increase in herbivory resulting from the heightened growth of plants due to the fertilizing effect of nutrients and  $\text{CO}_2$  in urban areas (Price, 1991). Alternatively, the 'predation proliferation' hypothesis (Sorace, 2002) proposes that certain predators can be adapted to urban environments, referred to as 'urban exploiters' in contrast to 'urban avoiders' (sensu Blair, 1996). This increase in abundance, coupled with the presence of exotic predators (Sasvári et al., 1995), can lead to an increase in predation pressure.

The above-mentioned studies conducted at regional or local scales illustrate that the effects of urbanization on both herbivory and predation are context-dependent and vary across regions. This variation could be associated with latitudinal gradients in biotic interactions, which are more intense at lower latitudes than at higher latitudes (The Herbivory Variability Network, 2023; Zvereva & Kozlov, 2021). This pattern might be explained by the 'latitudinal biotic interaction' hypothesis (Dobzhansky, 1950), which proposes that primary productivity and species richness increase in the tropics (Dobzhansky, 1950; Novotny et al., 2006), primarily due to warm temperatures all year-round (Coley & Aide, 1991). The consequences of this richness increase are that more productive ecosystems sustain larger levels of herbivory (McNaughton et al., 1989), while more diverse predator communities create redundancies and complementarity in prey consumption, resulting in an increase in predation ('Paine's predator' hypothesis; Paine, 1966). Despite the theoretical and empirical

background supporting the 'latitudinal biotic interaction' hypothesis (e.g. Garibaldi et al., 2011; Moreira et al., 2015; Pennings et al., 2009; Pennings & Silliman, 2005), the literature presents contradictory evidence about how the intensity of biotic interactions changes along the latitudinal gradient (Anstett et al., 2016). In the particular case of herbivory, some studies point to an increase in insect herbivory with latitude (Adams & Zhang, 2009; Del-Val & Armesto, 2010), while others report no latitudinal differences (Salazar & Marquis, 2012) or a peak at intermediate latitudes (Kozlov et al., 2015). In predation, Lövei and Ferrante (2017) found no effects of latitude on the strength of biotic interactions, whereas other studies found different and even opposite effects depending on the predator (Roslin et al., 2017; Zvereva et al., 2019).

Global-scale studies are necessary to produce general conclusions about how trophic interactions vary with urbanization and to understand how these effects change along the latitudinal gradient. To date, only a few studies have investigated how herbivory changes with urbanization along latitudinal gradients (Kozlov et al., 2017; Meineke et al., 2019; Moreira et al., 2019; Valdés-Correcher et al., 2022), and no studies have reported the respective patterns in predation. These studies conclude that urbanization leads to a reduction in herbivory, and that this effect does not change along the latitudinal gradient. However, it is important to note that these studies typically comprise small latitudinal gradients (10° to 20° latitudinal range) or use non-comparable categorical variables (urban–rural) as a proxy of urbanization, limiting the generalizability of their conclusions. To address this research gap, we investigated how trophic interactions (insect herbivory and bird predation) vary with human population density—a continuous proxy of urbanization—along a global latitudinal gradient. To achieve this goal, we compiled data on trophic interactions between plants, insects and birds worldwide, collected using similar (and thus comparable) protocols. Employing a broad latitudinal gradient spanning both hemispheres, our aim was to determine whether the effects of human pressure on trophic interactions are universal or change latitudinally. We expected a decrease in the intensity of trophic interactions with increasing urbanization, in line with the 'increased disturbance hypothesis', with higher impacts of urbanization at higher latitudes. To our knowledge, this is the first study exploring the effects of urbanization across latitudes on trophic interactions on a global scale.

## 2 | METHODS

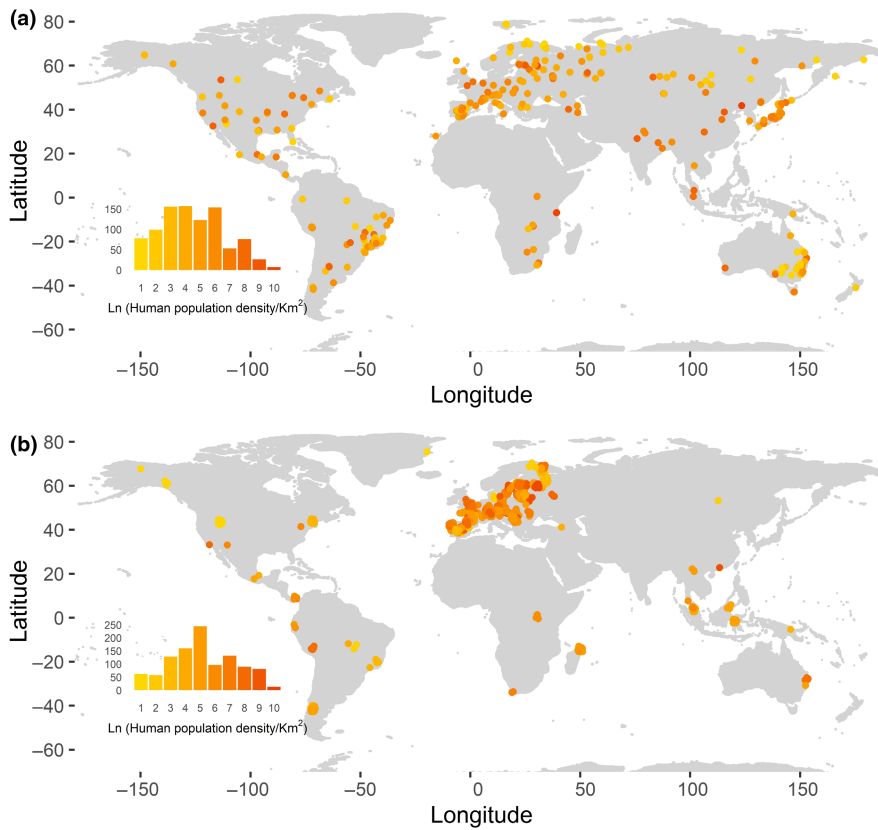
### 2.1 | Herbivory

We extracted the majority of our herbivory data from a systematic global review (Kozlov et al., 2015) and supplemented it with additional data published between 2015 and December 2021. The search was conducted on April 19, 2022, using the ISI Web of Science with the keywords "Defoliation" and "Insect herbivory" [i.e. Defoliation (All Fields) AND insect herbivory (All Fields) and 2021

OR 2020 OR 2019 OR 2018 OR 2017 OR 2016 OR 2015 (Publication Years)]. The keyword "Defoliation" was chosen to exclude other types of herbivory, such as galler herbivory or miner herbivory, while "insect herbivory" was added to exclude papers referring to vertebrate herbivores. Given the rapid changes in the human population, our analysis focused on data collected after 2000. We selected all papers where insect herbivory was measured as the proportion of leaf area consumed by defoliating insects, either through image software or visually, following the method proposed by Alliende (1989). Galler and miner herbivory were excluded from our analyses because they were not systematically included in the reviewed papers (e.g. Mendes et al., 2021). Our focus was solely on data related to herbivory on woody plants, using the same search criteria as Kozlov et al. (2015). From the 130 articles obtained, only eight used the selected methodology to quantify herbivory. We also incorporated data provided in Hernández-Agüero et al. (2024) (Figure 1a). A list of 10 sources can be found in [Supplementary Material 1 Table S1](#), and a comprehensive list of the studies reviewed (130 sources) along with the selection criteria is available in [Supplementary Material 2](#).

### 2.2 | Predation

We obtained predation data from two global studies (Roslin et al., 2017; Zvereva et al., 2019) and conducted a search for additional studies published between January 2000 and December 2021, using the ISI Web of Science on April 19, 2022. The search employed keywords "bird", "predation" and "larvae" or "caterpillar" [i.e. Results for 'bird (All Fields)' AND 'predation (All Fields)' AND 'larvae (All Fields) OR caterpillar (All Fields)' and '2021 OR 2020 OR 2019 OR 2018 OR 2017 OR 2016 OR 2015 OR 2014 OR 2013 OR 2012 OR 2011 OR 2010 OR 2009 OR 2008 OR 2007 OR 2006 OR 2005 OR 2004 OR 2003 OR 2002 OR 2001 OR 2000 (Publication Years)']. Bird predation on herbivorous insects was quantified using attack rates on artificial caterpillars made of odourless plasticine. These caterpillars were placed on woody plant branches or leaves. After an exposure period ranging from 2 to 64 days, the caterpillars were revisited, and bird peak marks were counted following the method proposed by Low et al. (2014). Most of the identified studies included caterpillars of different colours, except for Roslin et al. (2017), which employed green-coloured caterpillars exclusively. As prey colours can influence attack rates (Hernández-Agüero et al., 2020) and colour preferences by birds can change latitudinally, we specifically selected green caterpillar data, which does not show changes in preference by predators along latitudinal gradients (Zvereva et al., 2019). Our search identified 320 publications, among which only 13 studies shared similar methods to those of Roslin et al. (2017) and Zvereva et al. (2019) and provided raw data on green plasticine models. We also included the data from Hernández-Agüero et al. (2024) (Figure 1b). A list of 16 sources can be found in [Supplementary Material 1 Table S2](#), and a complete list of the studies reviewed and the criteria used for exclusion can be found in [Supplementary Material 2](#).



**FIGURE 1** Location of data from selected studies on (a) herbivory ( $n=408$  localities) and (b) predation ( $n=517$  localities). The yellow-red scale represents the natural logarithm of human population density. The histogram located at the bottom left of each figure represents the frequency of human population density on a ln-scale.

As the duration of the prey exposure period varied across studies, we standardized the predation rate, originally representing the rate of predation, to express it as the probability of a caterpillar attack occurring on any given day, considering the rate of attacks over a specific number of days (henceforth the probability of bird predation). This probability was calculated as:

$$P(X = 1) = 1 - P(X = 0) = 1 - \left[1 - (N_A/N_T)\right]^{(1/t)}$$

where  $X$  is a binary random variable denoting whether a caterpillar is attacked by birds or not.  $P(X=1)$  represents the probability of a caterpillar being attacked by birds on any given day, while  $P(X=0)$  represents the probability of no caterpillar being attacked by birds on any given day.  $N_A$  represents the number of caterpillars attacked,  $N_T$  is the total number of caterpillars deployed per period and  $t$  is the length of the period in days during which caterpillars were deployed. By raising  $(1 - N_A/N_T)$  to the power of  $(1/t)$ , we determine the complement of the predation rate ( $N_A/N_T$ ) for one day. Subtracting this value from 1 yields the probability of the event occurring on any given day. This formula accounts for the cumulative probability of the event not occurring over the observation period and then calculates the probability of it occurring on a single day.

### 2.3 | Human population and latitude

We used the Gridded Population of the World (GPWv4 2020) dataset, at 1 km spatial resolution, to estimate human population density

at each study site. Each site contained one to several observations of either herbivory or predation. To do so, we generated a 10km radius buffer at each site using the 'st\_buffer' function of the 'sf' package (Pebesma, 2018). This buffer size, which has been applied in other studies investigating the effects of human impact on vertebrate and plant species (Kim et al., 2003; Pautasso, 2007), exhibits a high correlation ( $r \geq 0.7$ ) with population density values obtained at smaller (e.g. 5 km radius buffer) and larger (e.g. 25 or 40km radius buffer) scales (Supplementary Material 1 Figures S1 and S2). Next, we cropped the rasterized GPWv4 dataset with our site buffer of 10km, employing the 'crop' function of the R package 'raster' (Hijmans, 2020). Subsequently, we created a new raster object using our buffered coordinates and the GPWv4 cropped dataset, applying the 'mask' function. Finally, we extracted the total human population at every site with the 'extract' function, and then human population density per  $\text{km}^2$  was calculated by dividing this total by the area in  $\text{km}^2$ . Human population density was correlated with other commonly used indices of urbanization, such as the proportion of built area (Pearson's  $r=0.73$ ,  $n=915$ ,  $p<0.001$ ; Supplementary Material 1 Figure S3), which was obtained from Dynamic World V1 (Brown et al., 2022). We employed absolute (i.e., unsigned) latitude, which exhibited a high correlation with mean annual temperature (Pearson's  $r=-0.83$ ,  $n=915$ ,  $p<0.001$ ; Supplementary Material 1 Figure S3). The mean annual temperature was estimated at each study site as the averaged values between 1970 and 2000. Climatic data were sourced from the WorldClim database (Fick & Hijmans, 2017) using the 'getData' function from the 'raster' package. No correlation was found between human population density and absolute latitude (Pearson's

$r = -0.07$ ,  $n = 915$ ,  $p = 0.023$ ; [Supplementary Material 1 Figure S3](#). Results of correlations for herbivory ([Figure S4](#)) and predation ([Figure S5](#)) can be found in [Supplementary Material 1](#).

## 2.4 | Data analyses

We employed generalized linear mixed models (GLMM) with a beta error distribution and a logit link function to explore the effects of human population and latitude on bird predation and insect herbivory. Beta is a family of continuous probability distributions defined on the interval  $[0, 1]$ , and therefore appropriate for the type of response variables we are modelling in this study. We used the natural logarithm of the human population, absolute latitude and their interaction as predictors. In the GLMMs for herbivory, we incorporated the following random factors: (i) site, which accounted for potential spatial autocorrelation (there were from 1 to 49 datasets per site); and (ii) plant species nested within genus, accounting for variations in palatability and plant defences against herbivory among plant taxa. In the GLMMs for bird predation, site was incorporated as a random factor (with data ranging from 1 to 12 observations per location) to address potential autocorrelation effects of repeated measures over time in the same location, which also includes memory/learning effects, where birds that already tried to feed on a fake caterpillar would tend to avoid them afterward (Svádová et al., 2009; Hernández-Agüero et al., 2020). All GLMMs were fitted using maximum likelihood with the function 'mixed\_model' of the R package 'glmmTMB' (Brooks et al., 2017).

For both herbivory and predation, alternative models were compared using the Akaike information criterion (AIC) to assess the effects of explanatory variables (i.e. fixed effects). Models with a difference in  $AIC > 2$  suggested that the less favourable model could be omitted. Following Nakagawa and Schielzeth (2013), we estimated the  $R^2$  of all plausible linear or mixed models. This approach allowed the calculation of two components of  $R^2$ : (1) a marginal  $R^2$  ( $R^2_m$ ) that considers only the variability explained by fixed effects; and (2) a conditional  $R^2$  ( $R^2_c$ ) that accounts for the variability supported by both fixed and random effects. To explore model residuals, we employed a simulation-based approach to generate

readily interpretable scaled (quantile) residuals for the fitted GLMMs (Hartig, 2019). Additionally, Moran's index was utilized to estimate spatial autocorrelation in model residuals, both for the proportion of herbivory and the probability of predation. To assess the significance of spatial autocorrelation, Moran's index was compared with a null model random distribution using the 'spdep' package (Bivand & Wong, 2018). In cases where spatial autocorrelation in model residuals was found to be significant, we re-fitted the model, incorporating a spatial autocorrelation function with an exponential correlation structure. This involved utilizing a Euclidean distance matrix based on site coordinates (Brooks et al., 2017). To ensure the robustness of our analyses, we repeated all procedures with human population density calculated at different buffer sizes (i.e. 1, 5, 10, 15, 20, 25, 30, 35 and 40 km radius buffer). This was done to verify that the spatial scale at which human population density was measured did not influence the outcomes of our analyses ([Supplementary Material 1 Tables S3 and S4](#)).

## 3 | RESULTS

### 3.1 | Herbivory

We combined information on herbivory from 508 woody plant species, representing 271 genera and 113 families, collected in 408 different localities spanning 122° latitude (from 43° S to 79° N). The range of human population density in these locations varied from 0 to 21,899 inhabitants/km<sup>2</sup>. The mean proportion of leaf area consumed was 0.0705 (CI95: 0.0644–0.0765). The best model explaining the observed variability in herbivory included human population density on the ln-scale (10 km radius buffer), absolute latitude and their interaction ([Table 1](#); [Supplementary Material 1 Table S5](#)). The values of conditional  $R^2$  (0.763) compared to marginal  $R^2$  (0.046) highlight the strong effect of plant species on determining herbivory pressure. Model residuals did not exhibit spatial autocorrelation (Moran I statistic standard deviation = -1.66,  $p = 0.95$ ).

The model predictions revealed varied patterns of insect herbivory in relation to human population density along the latitudinal gradient. In lower latitude localities (<-25°), herbivory decreased as the

**TABLE 1** Comparison of alternative models using the Akaike information criterion (AIC).

Model	Insect herbivory		Bird predation	
	AIC	$R^2_m/R^2_c$	AIC	$R^2_m/R^2_c$
Null model	-3933.74		-6882.27	
Abs (Latitude)	-3950.94		-6888.32	
Ln (Human population)	-3934.32		-6882.51	
Ln (Human population) + Abs (Latitude)	-3949.26		-6888.23	
Ln (Human population) * Abs (Latitude)	<b>-3954.79</b>	<b>0.046/0.763</b>	<b>-6896.21</b>	<b>0.010/0.032</b>

Note: The best model (lowest AIC) is indicated in boldface type.  $R^2_m$ , a marginal  $R^2$  that only considers the variability explained by fixed effects;  $R^2_c$ , a conditional  $R^2$  that accounts for the variability supported by both fixed and random effects.

human population increased. This effect diminished towards more temperate latitudes (approximately  $\sim 35^\circ$ ) and reversed at higher latitudes ( $>45^\circ$ ), resulting in higher herbivory in more populated areas (see Figure 2).

### 3.2 | Predation

We compiled data from 517 different localities spanning  $116^\circ$  latitude (from  $42^\circ$  S to  $74^\circ$  N), with a human population ranging from 0 to 12,401 inhabitants/km<sup>2</sup>. The mean probability of a plasticine caterpillar being attacked by a bird during one day of exposure was 0.0557 (CI95: 0.0654–0.0654). Similar to herbivory, there was a variation in the probability of bird predation with human population density on the ln-scale, absolute latitude and their interaction (10 km buffer; Table 1; Supplementary Material 1 Table S5). We detected spatial autocorrelation in model residuals (Moran I statistic standard deviation = 10.44,  $p < 0.0001$ ), so best-fit models were re-fitted, including a spatial autocorrelation structure.

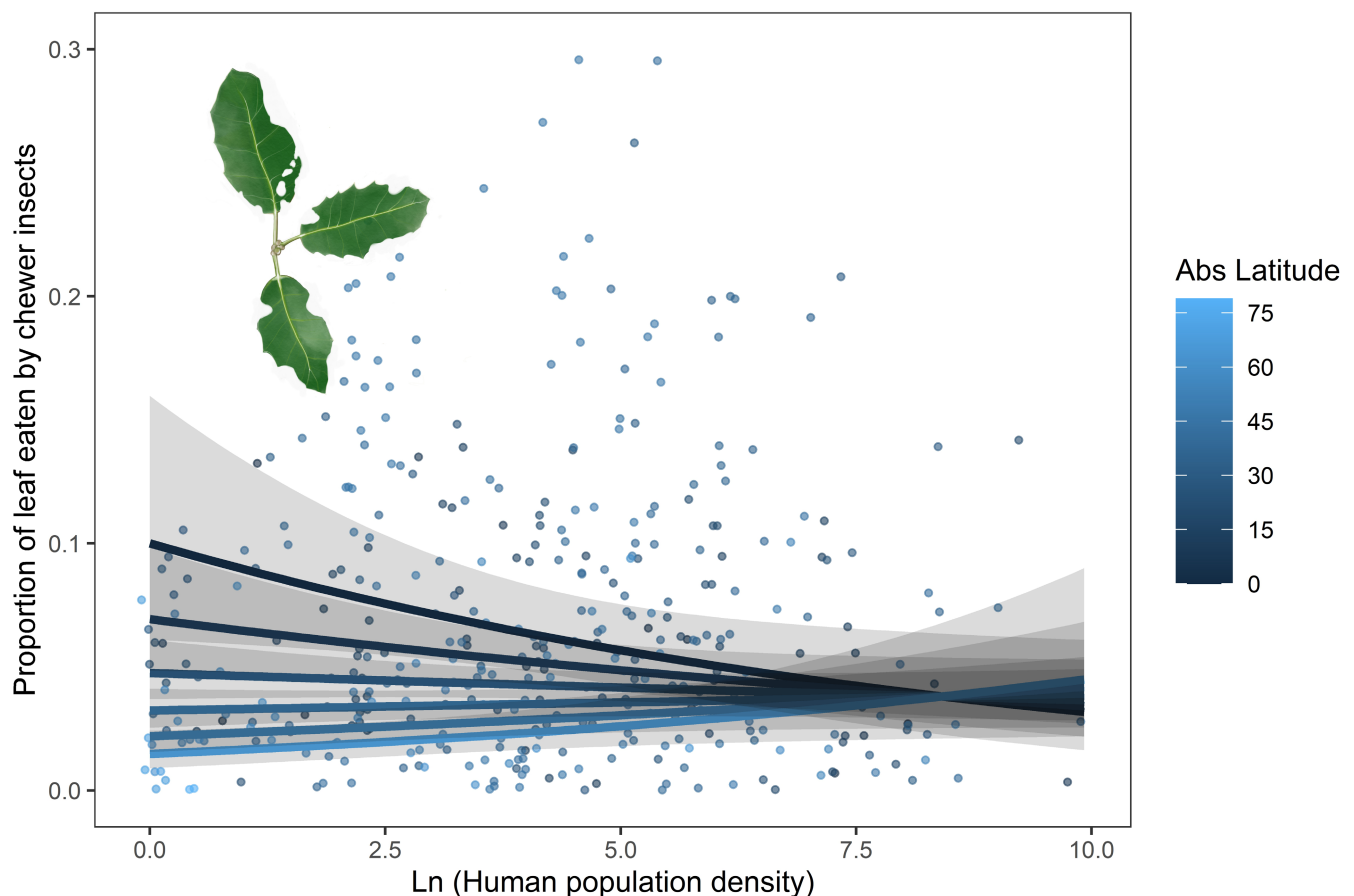
The model revealed changes in the probability of bird predation with the human population along the latitudinal gradient. For lower latitude ( $<40^\circ$ ) localities, there was a strong decrease in predation

as the human population increased. This trend weakened towards higher latitudes (subtropical and temperate ecosystems;  $\sim 50^\circ$ ) and reversed at even higher latitudes ( $>60^\circ$ ), indicating greater predation in more populated areas (Figure 3).

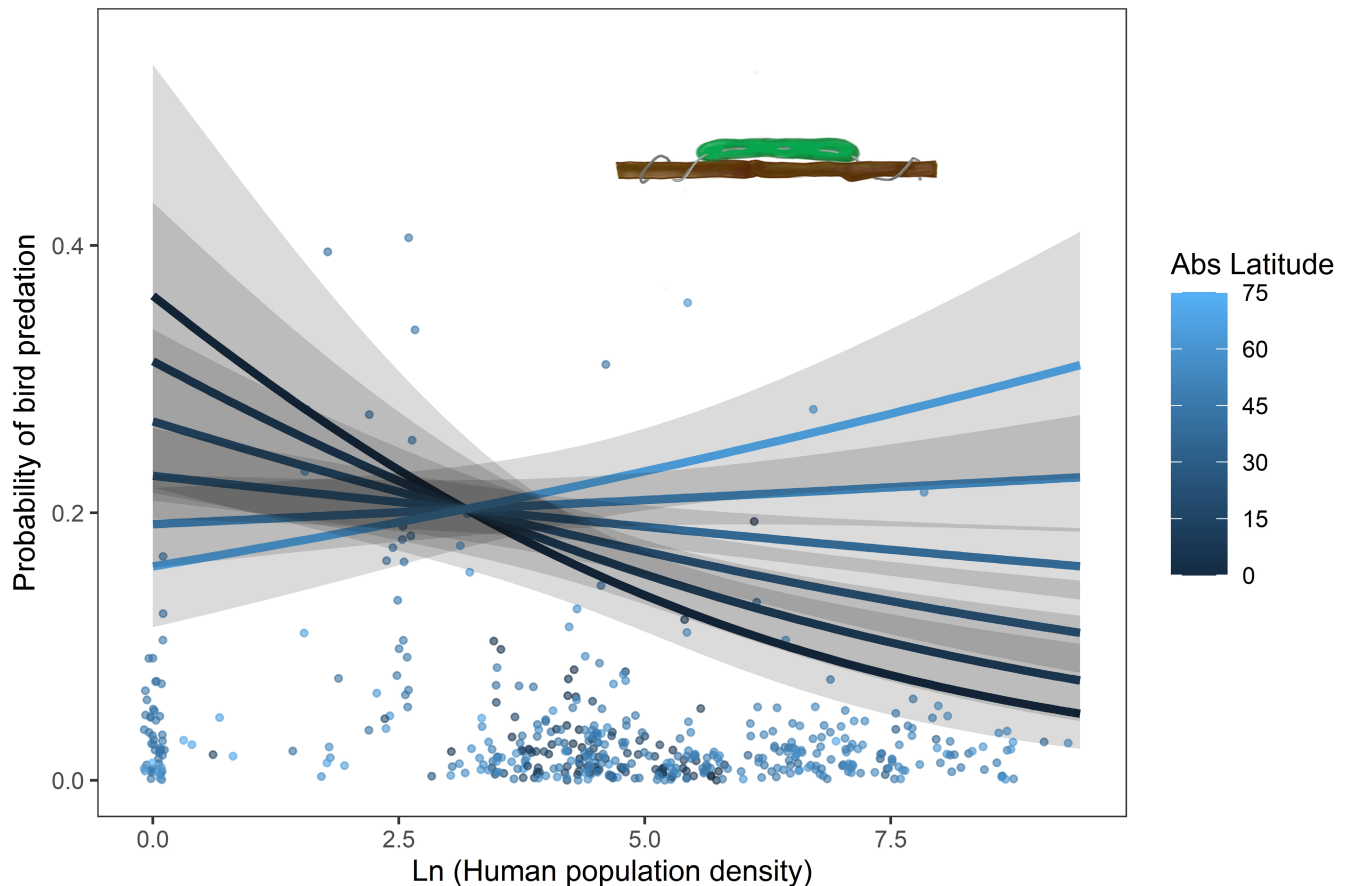
## 4 | DISCUSSION

We expected to find a decrease in both herbivory and predation with an increase in the human population, with this effect being less prominent at lower latitudes, where the intensity of biotic interactions is greater than at higher latitudes. Our results partly confirm our initial expectations, but unexpectedly, they reveal that the intensity of trophic interactions can in fact increase with the increase in urbanization at higher latitudes. So, whereas in tropical areas we detected the lowest rates of herbivory and predation in highly populated areas, this pattern becomes negligible in temperate regions and even reverses in higher latitudes, where herbivory and predation increased with increasing human population density.

At low latitudes, we observed a reduction in both herbivory and predation with an increase in human population density. The



**FIGURE 2** Predictions of generalized linear mixed models showing the proportion of herbivory with 95% confidence intervals along a gradient of human population density (on ln-scale) at six different absolute latitudes ( $0^\circ$ ,  $15^\circ$ ,  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$  and  $75^\circ$ ; marked by different colours). Mean observed values of the proportion of herbivory per plant species and site are shown by dots. Colour represent the absolute latitude.



**FIGURE 3** Predictions of generalized linear mixed models showing the probability of bird predation on green caterpillars with 95% confidence intervals along a gradient of human population density (on ln-scale) at six different absolute latitudes (0°, 15°, 30°, 45°, 60° and 75°; marked by different colours). The mean observed values of the probability of bird attack per site are represented as dots. Colour represent the absolute latitude.

vulnerability of predator and herbivore species to habitat alteration and loss caused by the growing human population aligns with the ‘increasing disturbance’ hypothesis (Eötvös et al., 2018). Examples of this phenomenon include diminished water resources, exposure to pollutants and toxins, collisions with structures or vehicles and limited food availability (Newton, 1998). The greater diversity of food resources may contribute to reduced predation and herbivory, especially among omnivore species. Consequently, this shift could lead to a decrease in the intensity of trophic interactions among native species, fostering the exploitation of introduced food sources or specific exotic animal and plant species (Schmidt, 1999). The presence of exotic species might also explain the decline in predation and herbivory through competition, disease transmission, or direct predation (Sasvári et al., 1995).

When examining only unpopulated or sparsely populated areas, we observed a decline in biotic interactions with increasing latitude, in line with the ‘latitudinal biotic interaction’ hypothesis (Dobzhansky, 1950). This pattern aligns with the concept that higher productivity supports increased herbivory (McNaughton et al., 1989), while diverse predator communities contribute to an increase in predation (‘Paine’s predator’ hypothesis; Paine, 1966). In contrast, plants at higher latitudes experience shorter growing

seasons and lower temperatures, resulting in, on average, less herbivory (Feeny, 1976).

At higher latitudes, densely populated areas exhibited elevated levels of both herbivory and predation. Higher herbivory levels could be explained by the ‘predator relaxation/safe habitat’ hypothesis (Noske, 1998) or the ‘natural enemy release’ hypothesis (Keane & Crawley, 2002). Both hypotheses suggest lower levels of herbivory in urban areas due to reduced predator presence, allowing herbivore species to proliferate. However, in our study, we observed an unexpected increase in both herbivory and predation in highly populated areas. The ‘plant stress’ hypothesis (White, 1969), suggesting that herbivory levels increase in disturbed areas due to a reduction in plant anti-herbivore defences, or the ‘plant vigour’ hypothesis (Price, 1991), proposing an increase due to enhanced plant growth from the fertilizing effect of urban nutrients, could help explain our results for higher latitudes. However, with the available data, we cannot discern which hypothesis prevails. For predation, the ‘predation proliferation’ hypothesis (Sorace, 2002) explains that certain predators can adapt to urban environments, known as ‘urban exploiters’ in contrast to ‘urban avoiders,’ which helps increase their abundance and, consequently, predation pressure. This could potentially explain the patterns found in higher latitudes, although no previous study

has reported differences in the increase in abundance of urban exploiters along the latitude.

Overall, the opposite patterns of herbivory and predation with urbanization in tropical versus polar latitudes could be explained by climatic changes produced in urban areas, such as the Urban Heat Island effect (Kim, 1992). Cities can be up to 10°C warmer than surrounding rural areas. This effect is greater at higher latitudes (Wienert & Kuttler, 2005) and can be easily detected more than 10 km away from the city centre (Peng et al., 2020). The Urban Heat Island effect might facilitate ectotherm insect activity. Species at higher latitudes are better positioned to endure climate change, as lower temperatures act as a limiting factor for the performance and survival of these species (Deutsch et al., 2008). Consequently, in cities with cooler climates, the seasonal period of insect activity may be longer compared to sparsely populated areas (Youngsteadt et al., 2015). This extended activity period could potentially counterbalance the adverse effects of urbanization observed in warmer latitudes (Youngsteadt et al., 2017). The Urban Heat Island effect, creating artificially warmer conditions during winter, may promote vegetation growth in higher latitudes, whereas its impact may diminish in lower latitudes where growth is less seasonal (Peng et al., 2011). The rise in temperature can impact the activity of tropical insects, given their tendency to be thermal specialists adapted to relatively stable environmental temperatures throughout the year (Sunday et al., 2011). Consequently, this specialization contributes to higher constancy in biotic interactions in the tropics, as observed in studies on herbivory (The Herbivory Variability Network, 2023) and predation (Hernández-Agüero et al., 2024). So, whereas at mid-latitudes, the benefits of increasing temperatures counterbalance the negative influence of human impacts, at higher latitudes the positive effects exceed the negative ones. The potential increase in the abundance of ectothermic insects in highly populated areas at high latitudes could ultimately result in higher populations of insectivorous birds through bottom-up mechanisms (Polis et al., 1997). This helps to explain why we observed similar interactions between human population density and latitude for both herbivory and predation.

Recently, researchers have investigated the relationship between urbanization and latitude concerning herbivory in both Europe (Kozlov et al., 2017; Moreira et al., 2019) and the USA (Meineke et al., 2019). In contrast to our findings, these studies showed that there was a decrease in chewing herbivory with increasing urban population throughout a latitudinal gradient. The discrepancies between the results reported in these studies and our findings might be related to the larger latitudinal range covered by our study (122°; or 74° of absolute latitude gradient). In addition, some of these studies encompassed smaller ranges in human population density than our study (e.g. Meineke et al., 2019) or included human use categories instead of population density as a surrogate of human impact on the territory (e.g. Kozlov et al., 2017; Moreira et al., 2019), which precludes direct comparison with our results.

Given that cities currently exhibit temperatures that might be experienced outside of urban areas at the same latitude in the future

(Youngsteadt et al., 2015), and based on our results, we anticipate a decrease in the intensity of trophic interactions at tropical latitudes, as predicted in Kozlov and Zvereva (2015), no effects at temperate latitudes, and an increase of trophic interactions in cold latitudes in response to climate change. This could have significant implications for ecosystem services (e.g. nutrient cycling, pest control) that would impact tropical and cold regions differently, potentially disrupting the natural balance of ecosystems (i.e. ecological imbalance). These differences between cold and tropical latitudes are noteworthy, especially considering the projected concentration of new big cities (5–10 million people) in tropical latitudes in the next 10 years (United Nations, 2018), which may lead to detrimental consequences for trophic interactions and the ecosystem services they provide. Further experimental research is needed to determine whether the patterns identified here, termed the 'opposite latitudinal-disturbance' hypothesis (Alonso-Crespo & Hernández-Agüero, 2023), can be explained by the differential effects of changes in climatic characteristics in urban areas worldwide. It is essential to unravel the mechanisms underlying the observed patterns to draw sound conclusions about the potential impact of new urban areas or global climate changes on the interactions among species.

## 5 | CONCLUSIONS

In conclusion, our study reveals that changes in trophic interaction intensity with an increasing human population density are contingent upon latitude. Increasing human population density at high latitudes has a positive effect on herbivory and predation pressure, while the opposite trend is observed at low latitudes. Various hypotheses have been proposed to explain these results, and further research is needed to disentangle the mechanisms underlying these patterns. These results open a new venue for studying the effects of human impacts on different ecosystem properties across latitudinal gradients.

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### CONFLICT OF INTEREST STATEMENT

The authors confirm to not have any conflict of interest.

### DATA AVAILABILITY STATEMENT

All the data and R scripts used in this study are available at Dryad: "The effects of human population density on trophic interactions are contingent upon latitude": <https://doi.org/10.5061/dryad.sbcc2frfc>.

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## BIOSKETCH

Juan A. Hernández-Agüero is interested in studying the effects of land-use changes on trophic interactions such as herbivory or bird predation, behavioural ecology in different groups of vertebrates, conservation biology and biocultural diversity among other facets of biodiversity.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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