

Trophic cascades in tropical rainforests: Effects of vertebrate predator exclusion on arthropods and plants in Papua New Guinea

Marketa Houska Tahadlova^{1,2}  | Ondrej Mottl³  | Leonardo R. Jorge¹ | Bonny Koane⁴ | Vojtech Novotny^{1,2,4} | Katerina Sam^{1,2} 

¹Laboratory of Multitrophic Interactions, Biology Centre of Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic

²Faculty of Sciences, University of South Bohemia, Ceske Budejovice, Czech Republic

³Department of Biological Sciences and Bjerknes Centre for Climate Research, University of Bergen, Bergen, Norway

⁴The New Guinea Binatang Research Centre, Madang, Papua New Guinea

Correspondence

Marketa Houska Tahadlova, Laboratory of Multitrophic Interactions, Biology Centre of Czech Academy of Sciences, Institute of Entomology, Branisovska 31, Ceske Budejovice 370 05, Czech Republic.
Email: marketa.tahadlova@entu.cas.cz

Funding information

Grantová Agentura České Republiky, Grant/Award Number: 18-23794Y; H2020 European Research Council, Grant/Award Number: BABE 805189

Associate Editor: Ferry Slik

Handling Editor: Michael Staab

Abstract

Insect herbivores have the potential to consume large amounts of plant tissue in tropical forests, but insectivorous vertebrates effectively control their abundances, indirectly increasing plant fitness accordingly. Despite several studies already sought understanding of the top-down effects on arthropod community structure and herbivory, such studies of trophic cascades in old tropics are underrepresented, and little attention was paid to top-down forces in various habitats. Therefore, we examine how flying insectivorous vertebrates (birds and bats) impact arthropods and, consequently, affect herbivore damage of leaves in forest habitats in Papua New Guinea. In a 3-month long predator enclosure experiment conducted at four study sites across varying elevation and successional stage, we found that vertebrate predators reduced arthropod density by ~52%. In addition, vertebrate predators decreased the mean body size of arthropods by 26% in leaf chewers and 47% in non-herbivorous arthropods but had only a small effect on mesopredators and sap suckers. Overall, the exclusion of vertebrate predators resulted in a ~41% increase in leaf damage. Our results, across different types of tropical forests in Papua New Guinea, demonstrate that flying vertebrate insectivores have a crucial impact on plant biomass, create a selective pressure on larger and non-predatory prey individuals and they prey partition with mesopredators.

KEYWORDS

herbivory, Intraguild predation, top-down control, vertebrate predator exclusion

1 | INTRODUCTION

Biotic interactions are crucial processes that shape tropical terrestrial ecosystems (Paquette & Hargreaves, 2021). Insect herbivores, the most important primary consumers in tropical forests, consume between 10 and 40% of total leaf area annually (Coley & Barone, 1996), thus playing a decisive role in ecosystem functioning.

The top-down control of insect densities by insectivorous predators has been proposed by several authors as an invaluable “ecological service” for human well-being (e.g., Philpott et al., 2009; Sekercioglu, 2006; Zvereva et al., 2019). The role of insectivorous vertebrates in ecosystem functioning is receiving increasing attention but the net effect of top-down control by such insectivores remains unclear. In addition, almost half of the existing studies—42%

(26 out of 61)—on trophic interactions in the tropics have focused on agricultural sites in the Neotropics (Sam et al., 2022) and these results do not necessarily reflect the reality in richer natural sites, such as primary tropical forests. With the rapid destruction of tropical forests and the threat of global anthropogenic climate change, a greater understanding of the importance of these interactions, and how they might be affected by predicted ecosystem transformation, is essential to inform sensible conservation of such habitats (Coley & Barone, 1996; Gibson et al., 2011; Roels et al., 2018; Romero et al., 2021).

There is increasing evidence that insectivorous vertebrates have the capacity to directly suppress the abundance of herbivorous insects (e.g., Cassano et al., 2016; Kalka et al., 2008; Maas et al., 2013, 2019; Mooney et al., 2010), and thus, indirectly suppress the resulting leaf damage (e.g., Atlegrim, 1989; Greenberg et al., 2000; Mäntylä et al., 2011; Marquis & Whelan, 1996; Sanz, 2001). Some studies, however, found negligible effects cascading from insectivorous vertebrates to plants (e.g., Karp & Daily, 2014; Mooney, 2007), which suggests the ecological mechanisms involved are complex. Likely, the proposed complexity in the function of trophic cascades is composed of several factors playing various roles. For example, overall top-down control of lower trophic levels by predators is composed of separate effects caused by various vertebrate and invertebrate predators, and modified further by intraguild predation, insect herbivore community structure, and habitat characteristics. In a four-level system, the top predators and herbivores are supposedly limited by competition while the mesopredators, herbivores, and primary producers are limited by predation/herbivory (Preisser, 2008). Tropical rainforests are such an example of a four-level system comprised of highly complex food webs (Novotny et al., 2010).

Interactions between predators lead to a combined effect of multiple predators which is higher or lower than the sum of effects of individual predators (Chase et al., 2002; Ives et al., 2005). Increasing predator diversity could promote trophic cascades if predator species act synergistically (Cardinale et al., 2003; Losey & Denno, 1998) or additively (Snyder & Ives, 2003; Straub & Snyder, 2006), or dampen trophic cascades if these species engage in intraguild predation (Finke & Denno, 2003; Polis et al., 1989; Vance-Chalcraft et al., 2007). The relative importance/turnover of (meso)predators in insect herbivore suppression may also vary with changing environmental conditions (Gunnarsson, 2007; Sam et al., 2015, 2022; Sam & Koane, 2020).

The simultaneous consumption of arthropod mesopredators and herbivores should weaken or counterbalance, in part or in whole, the effect of vertebrate insectivorous predators on plants (Sam et al., 2022). The global meta-analysis of Mooney et al. (2010) showed that vertebrate insectivores acting as intraguild predators reduced predatory arthropods (by 38%) as well as herbivorous arthropods (by 39% respectively). Of particular interest, may be selective predation on particular arthropod taxa or, more simply, a preference for larger (and energetically more rewarding)

individuals. Birds, for example, have been shown to reduce the mean size of caterpillars by 12% by selectively feeding on larger individuals (Singer et al., 2017). Similarly, Karp and Daily (2014) found that predation by birds and bats reduced the average size of Araneae, Formicidae and arthropod larvae in large coffee plantations in Costa Rica.

Finally, the top-down effect size relates to primary productivity and other habitat characteristics. Highly diverse ecosystems (such as tropical rainforests) are, in terms of primary producers, the result of lower habitat filtering and higher competition for sources and natural enemies compared with less diverse ones (such as temperate forests; Wright, 2002; Bagchi et al., 2014). Conversely, the bottom-up effects of increased productivity of the basal trophic level may influence the strength of top-down control in a system, and thus, the patterns of biomass accumulation at subsequent trophic levels (Oksanen et al., 1981). Furthermore, Terborgh (2015) emphasized that in highly diverse ecosystems, such as tropical forests, we can observe variability in productivity and diversity caused by habitat filtering along ecological (e.g., vertical, elevational and disturbance/fragmentation) gradients. Additionally, the predation/competition trade-off may vary in a systematic fashion along such gradients. That is why understory plant biomass might be more valuable in primary rather than in secondary tropical rainforest or in primary tropical montane forest (Roslin et al., 2017). However, there are contradictory findings showing a strong connection between primary productivity and top-down control by vertebrate predators (Van Bael & Brawn, 2005) or weak (e.g., Halaj & Wise, 2001; Mooney et al., 2010; Philpott et al., 2009). Thus, the effect of habitat on trophic cascade strength in highly diverse tropical communities remains unclear.

As food web diversity increases, both the number and importance of higher trophic levels increase as they maintain diversity (Terborgh, 2015). This leads to an increased number of predator-prey interactions, and a corresponding rise in the relative importance of predation in structuring the community (Chan & Banks-Leite, 2020; Roels et al., 2018). As a result, more diverse communities should be structured primarily by predation, while competition should play a predominant role in less diverse food webs (Preisser, 2008). Contrary to this, empirical studies seem to support the exact opposite patterns, in other words, less diverse communities (“food chains”) are more likely to show strong top-down control (e.g., Belovsky & Slade, 1993; Halaj & Wise, 2001; Mazia et al., 2009; Mooney, 2007), while more diverse communities (“food webs”) tend to diffuse top-down control and be more affected by bottom-up factors (e.g., Fáveri et al., 2008; Gruner, 2004).

Such contradictions in results in comparison with predictions suggest possible variability in the extent to which vertebrate insectivores play roles as main and intraguild predators. Neglecting these issues may modify conclusions about the direct effects of vertebrate insectivores on arthropod communities and, indirectly, on plants. Nevertheless, we are not aware of any experimental exclusion studies which have addressed the impact of predators on entire

arthropod assemblages and herbivory across several habitat types of tropical rainforests (Sam et al., 2022).

Here, we focus on the effects of flying vertebrate insectivores (birds and bats; hereafter “vertebrate predators”). We examine the impacts of these invertebrate predators on arthropod density, guild composition and body size across entire whole arthropod assemblages and their indirect, flow-on, effects on plant damage. To determine whether and/or to what extent anthropogenic disturbance or elevation affect predatory pressure caused by vertebrate predators, we have focused on tree saplings growing in the understory of four different tropical forest habitats in Madang Province, Papua New Guinea.

We predict that

1. The exclusion of vertebrate predators will affect the density of arthropods, as well as plant herbivory.
2. This effect of vertebrate exclusions will be stronger in a primary montane forest compared to primary lowland forest due to the enhanced importance of top-down control by vertebrate predators at higher elevations (in contrast to the impacts of mesopredators).
3. The effect of the depauperate assemblages of vertebrate predators in disturbed habitats will be lower or absent compared with their effect in primary forest.
4. The exclusion of vertebrate predators will lead to increased density and mean body size of mesopredators and leaf chewers but will have a weak effect on other guilds (e.g., sap suckers) that are rarely eaten by vertebrates.
5. The ratios of mesopredators to other arthropods and mesopredators to leaf chewers (both—abundance and body size), will not change as vertebrate predators tend to be generalists, feeding equally on predators as well as other arthropods.

2 | METHODS

2.1 | Study sites

We conducted our study in four tropical forest habitats in Papua New Guinea. These were (1) “Primary lowland” (5°13.50'S, 145°04.91'E, 200 m asl)—undisturbed forest situated within >10,000 ha of contiguous lowland primary forest in the Wanang Conservation Area; (2) “Secondary lowland” (5°13'30.0" S 145°04'54.6" E, 200 m a.s.l.)—secondary successional vegetation following swidden agriculture surrounding Wanang village located at the border of the Wanang Conservation Area; (3) “Primary fragment” (5°01.73'S, 145°46.01' E, 200 m asl) a forest habitat within a fragment (ca. 1200 ha) of primary forest near the villages of Rempi and Baiteta situated in a landscape mosaic of secondary forests and swidden agriculture; and, (4) “Primary montane” (6°9.77'S, 146°50.37' E, 1700 m a.s.l.)—a continuous lower-montane primary rainforest in the YUS Conservation Area (Saruwaged Mountains, close to Kotet Village (Figures S1 and S2)). All studied habitats have a humid climate with a mild dry season from July to September;

average annual rainfall is 3600 mm. Experiments at all study sites were conducted between May and October 2012.

2.2 | Experimental design

In each habitat, within approximately 1 ha area, we selected 10 pairs of saplings with between one and four pairs of each selected plant species (80 saplings in total). All saplings elected were similar in height and crown size. We put emphasis on picking up abundant tree species. In the lowland sites we used: *Ficus bernaysii* King, *F. hahliana* Diels (Moraceae), *Litsea timoriana* Span. (Lauraceae) and *Syzygium nutans* (K.Schum.) Merr. and L.M.Perry (Myrtaceae). In the montane plots, we used the same species of *Ficus* and *Litsea* but had to substitute *Syzygium furfuraceum* Merr. for *S. nutans*. We analyzed both *Syzygium* spp. species together.

Within each pair of saplings, one individual was placed in an enclosure, and one acted as a control. Mean sapling height at the start of the experiment was 2.70 m for both enclosures and control. The mean leaf area per sapling differed across habitats: 0.83 ± 0.11 (\pm SD) m² in primary lowland, 0.38 ± 0.05 m² in primary montane, and 0.50 ± 0.06 in secondary lowland and 0.58 ± 0.09 in primary fragment.

The vertebrate predator enclosures for entire saplings were constructed with untreated PVC pipes (1.5 cm in diameter, 2 × 2 × 3 m) and covered with agricultural netting (mesh opening 2 × 2 cm; Figure S3). Each enclosure surrounded a volume of ca. 12 m³, which enclosed an average of $0.58 \pm$ SD 0.043 m² of leaf area. The materials used for enclosures did not attract arthropods, did not damage leaves or branches, and did not significantly reduce light (as recommended by Van Bael et al., 2003). To ensure equal disturbance of arthropod assemblages, we removed all arthropods from control and experimental saplings. The establishment of the enclosures, which took place in June 2012 (primary and secondary lowland), September 2012 (primary fragment) and October 2012 (primary montane).

Ninety days (\pm 3 days) after the establishment of the experiment, destructive censuses of arthropods and leaves were carried out. To harvest arthropods, field assistants covered the entire crown of each sapling to be sampled with a mosquito net (Figure S3). Once completely enclosed, the crown foliage and sapling stems were sprayed with a fast knockdown insecticide (Mortein®). All arthropods (ca. 1 mm length and above) were collected, their body lengths measured (mm), and identified to one of four feeding groups: leaf chewers (CHEW), sap suckers (SUC), mesopredators (PRE), and non-herbivorous arthropods (NR). In order to discern the overall effects of vertebrate insectivores on arthropod communities, we used density (Figure 2) and mean body size (Figure 4), while for the relative differences within the arthropod community and trophic cascade, we computed mean density and mean body size for control versus enclosure ratio (Table S1), and abundance and body size ratio of respective guilds (Figures S6 and S7). Both mean body size and density ratios are important in relationship to herbivory. If the predatory pressure caused by mesopredators changes it will translate into ratio

change, which, as a consequence, can enhance or weaken herbivory. The ratios were always computed in the same fashion. As an example, we present a simple formula for mean body size ratio of mesopredators and leaf chewers (Figure S8):

$$= \frac{\text{Mean body size of mesopredators}}{\text{Mean body size of mesopredators} + \text{Mean body size of leaf chewers.}}$$

2.3 | Leaf area and herbivory

We harvested all leaves from the branches, weighed them and arbitrarily selected ~400 leaves from each sapling (pulled blindly from a garbage bag). These were spread out on a white cardboard sheet (50×50cm), photographed and weighed (Figure S3), creating “leaf frame.” For each leaf photograph, we analyzed leaf area and leaf herbivory damage by chewing insects (hereafter “herbivory damage”) of all photographed leaves using ImageJ® and Photoshop® (Figure S3). Using Adobe Photoshop CS6 (Adobe Systems Inc), we outlined the missing edges on the photographed leaves based on their expected shape (Sam et al., 2020). ImageJ version 1.47 (National Institute of Health) was then employed to calculate the actual leaf area (a, in cm²), the reconstructed leaf area without any herbivore damage (b, in cm²), and the area lost to herbivory (c = b - a). We then estimated the percentage of leaf area loss as c/b*100 (Sam et al., 2020). The “mean herbivory damage” is therefore the percentage of the total leaf area lost due to consumption by herbivores across the scanned leaf area from each sapling, averaged across the saplings within a habitat type.

For the total leaf area per sapling, we first calculated their specific leaf area (SLA) using the total leaf area of scanned frames and their weight. We estimated leaf area of each sapling from the SLA and the total weight of all leaves collected from the given sapling. The obtained total leaf area was used to calculate arthropod density (abundance per m² of leaf area).

2.4 | Data analyses

To select the best predictors for each selected dependent variable, we followed a simple procedure. We created a generalized linear model (glm), a linear mixed model (lmm), or a generalized linear mixed model (glmm) using the lme4 (Bates et al., 2015) or glmmTMB package (Brooks et al., 2017). This “full model” lmm or glmm contained the variables Habitat (factor of four levels), Treatment (factor of two levels), Species identity (factor of four levels), and all their possible interactions. Tree identity was treated as a random effect. Model fit was then analyzed using the check_model and check_distribution functions from the performance package (Lüdecke et al., 2020) and the distribution of residuals was examined visually. To reduce unnecessary predictors, we used the dredge function from the MuMIn package (Barton, 2022), which creates a model for each possible combination of each predictor and selects the best model by parsimony (AICc). AIC of the resulting models were compared using function

AICtab (package bbmle, Bolker & R Development Core Team, 2020) and the best model was selected based on lowest delta AIC. When the best model was picked, we analyzed the model fit again using the aforementioned check_model and check_distribution functions, followed by visual examination of the distribution of residuals. For the final model, we tested included effects by conditional F-tests with the Kenward-Roger approximation or Chi-square tests and obtained estimated marginal means (= emmeans) and comparisons among all variable levels, using the emmeans package (Lenth, 2020). The most parsimonious models are included in Table 1.

This procedure was used to select the best predictors affecting: (i) total leaf area of saplings (Gamma error distribution; glmmTMB model), (ii) mean herbivory damage per sapling (average [percentage of leaf area]/100; beta error distribution; glmmTMB model), (iii) arthropod density per sapling (Gaussian error distribution, lmer model), (iv) density of mesopredator-others and mesopredators-leaf chewers ratios (binomial error distribution, glm model), (v) body size of arthropods per sapling (Gaussian error distribution, lmer model), and, (vi) arthropod body size ratio (Gaussian error distribution, lm model).

The model selection procedure was used to select the best predictors for: (i) total leaf area of saplings (Gamma error distribution; glmmTMB model), (ii) mean herbivory damage per sapling; beta error distribution; glmmTMB model, (iii) arthropod density per sapling (Gaussian error distribution, lmer model), (iv) ratio of individuals in the mesopredator guild on sapling (binomial error distribution, glm model), (v) size of arthropods per sapling (Gaussian error distribution, lmer model).

All analyses were conducted in R version 4.0.1. (R Core Team, 2021).

3 | RESULTS

3.1 | Herbivory

Herbivory per sapling varied between 1.71% and 17.69% and the mean herbivory per sapling was 7.54% (SEM = 0.41). There were general differences in herbivory between species (Chi² = 15.52, df = 3, p = .0014), between habitats (Chi² = 11.42, df = 3, p = .0096) and treatments (Chi² = 17, df = 1, p < .001). As predicted in H1, the control saplings suffered from ~6.2% (SEM = 0.4) herbivory, whilst enclosed saplings from ~8.8% (SEM = 0.49; Figure 1a). Saplings of *Litsea timoriana* and *Syzigium* spp. suffered from higher herbivory than *Ficus bernaysii* (Tukey HSD, P_{adj} = 0.002 for *Litsea* and P_{adj} = 0.013 for *Syzigium*; Figure 1b), but none of the species significantly differed in herbivory from *Ficus hahliana*. Saplings in the primary lowland forest understory suffered higher herbivory than saplings in primary montane (Tukey HSD, P_{adj} = 0.032) and primary forest fragment (Tukey HSD, P_{adj} = 0.01) but did not differ from the secondary forest (Figure 1c). Raw data (Figure S5) also suggest substantially higher herbivory in enclosures in primary lowland and primary montane forest.

TABLE 1 Model selection overview for leaf area, herbivory leaf damage, arthropod density (abundance per square meter of foliage), abundance ratio of mesopredators versus other groups, and arthropod body size

Model predictors	Leaf area	Herbivory	Density	Ratio	Size
Hab + Spec + Treat + Hab:Spec + Spec:Treat	27.42	15.59	NR	NR	NR
Hab + Treat + Guild + Guild:Treat + Guild:Hab	NR	NR	0.00	NR	0.00
Hab + Spec + Treat + Spec:Treat	10.17	5.27	NR	NR	NR
Hab + Spec + Treat + Hab:Spec	19.47	8.40	NR	NR	NR
Hab + Spec + Hab:Spec	16.56	12.77	NR	NR	NR
Hab + Treat + Hab:Treat	3.15	14.87	100.80	0.58	321.58
Hab + Spec + Treat + Guild	NR	NR	24.40	NR	NR
Hab + Treat + Guild	NR	NR	7.62	NR	129.98
Hab + Spec + Treat	4.71	0.00	38.09	NR	NR
Hab + Treat	1.95	7.85	135.81	0.00	318.82
Guild	NR	NR	44.81	NR	135.97
Treat	14.81	10.81	150.58	11.54	313.23
Hab	0.00	10.35	149.19	24.63	331.85
null	12.99	13.01	160.69	35.98	326.12

Note: The values represent dAIC of the respective models, where zero represents the best model (see Section 2) and “NR” represents not relevant predictors for the respective analysis. dAIC values of the final models are in bold.

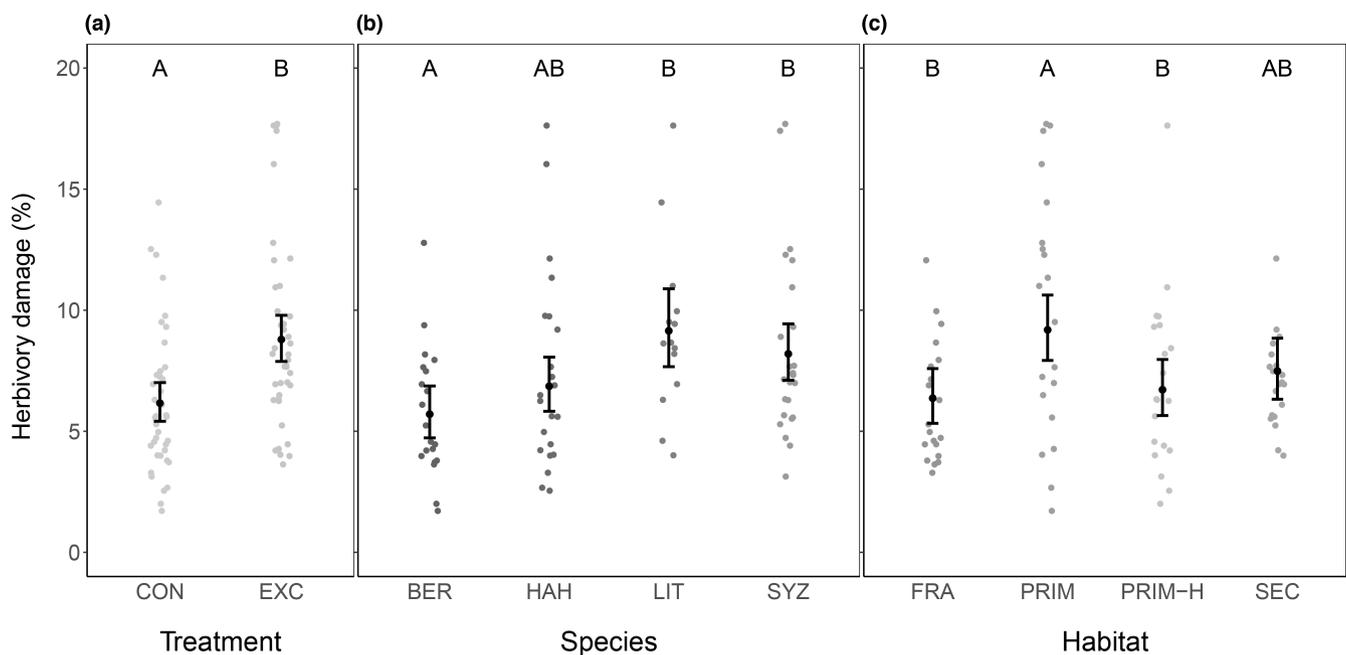


FIGURE 1 The effect of (a) treatment, (b) tree species and (c) habitat on leaf herbivory damage. Each point represents observed value per sapling. Thick points and whiskers represent estimated marginal means and their 95 percent quantile. Significant pairwise comparison between predictor with more levels were tested by Tukey post hoc tests and are indicated with letters. CON – Control, EXC – Exclusion, BER – *Ficus bernaysii*, HAH – *Ficus hahliana*, LIT – *Litsea timoriana*, SYZ – *Syzigium* spp., FRA – primary forest fragment, PRIM – primary lowland forest, PRIM-H – primary montane forest, SEC – secondary forest

3.2 | Arthropod density and ratios

We collected a total of 2341 arthropod specimens (29.3 ± 1.09 individuals per sapling) and there was a 52% higher density of arthropods on enclosed saplings (Kenward-Roger $F_1 = 6.69$, $p = .012$). Unexpectedly, however, the exclusion of vertebrate predators led

to a significant increase in density of leaf chewers (Tukey HSD, $P_{adj} = 0.017$) and other arthropods (Tukey HSD, $P_{adj} < 0.001$), and to a non-significant increase in density of mesopredators and sap suckers (Figure 2a). Contrary to expectations (H5), this pattern was also evident in the abundance ratios comparing mesopredators to all other guilds (Figures 3, S6 and S7)

In contrast to our hypotheses (H2, H3), arthropod density in primary lowland forest was significantly lower (by 46%, Tukey HSD, $P_{adj} = 0.015$) than in primary fragment forest but there was no significant difference from primary montane and secondary lowland forest. We also detected differences in density among guilds within respective habitats (Guild x Habitat: $F_9 = 3.061, p = .002$, Figure 2b). In the primary lowland forest, arthropod densities were balanced across guilds, while in primary lowland fragment and secondary lowland forest the communities were dominated by mesopredators. In primary montane forest, other arthropods and mesopredators dominated in the communities. The abundance ratios of mesopredators-others (Figure 3) and mesopredators-leaf chewers (Figure S7) declined when vertebrate predators were absent. The decrease in the ratio was consistent in the exclosures across all the studied habitats (Figure S6). Exceptionally, however, the mesopredators-others ratio was significantly lower in primary montane forest compared with primary fragment and secondary lowland forest, but none of the habitats were different from primary lowland forest (Figure 3b). On the level of a single taxon control-exclosure ratio, mesopredatory

taxa increased in exclosures only in secondary lowland forest (Formicidae, Opilionidae and Araneae), but there were ratios around 0.5 or lower in other habitats, suggesting a neutral or negative effect of the exclusion of vertebrate predators (Table S1).

3.3 | Arthropod body size

The arthropod body size varied from 1 to 70mm with the median size 5 mm (mean = 7.29). The largest individuals were species of Phasmatoidea (~55.5 mm) and Mantodea (~20mm), the smallest ones, Margarodidae and Thysanoptera (~1 mm). As expected in H4 arthropod individuals were larger by 27% on the saplings from which vertebrate predators had been excluded (Kenward-Roger $F_1 = 12.76, p < .001$). In contrast to our predictions, the effect of vertebrate predators, differed among guilds (Kenward-Roger $F_3 = 2.59, p = .05$). The body size was 26% larger in leaf chewers (Tukey HSD, $p = .002$) and 47% in other arthropods (Tukey HSD, $p < .001$). Non-significant increases were observed in mesopredators and sap suckers

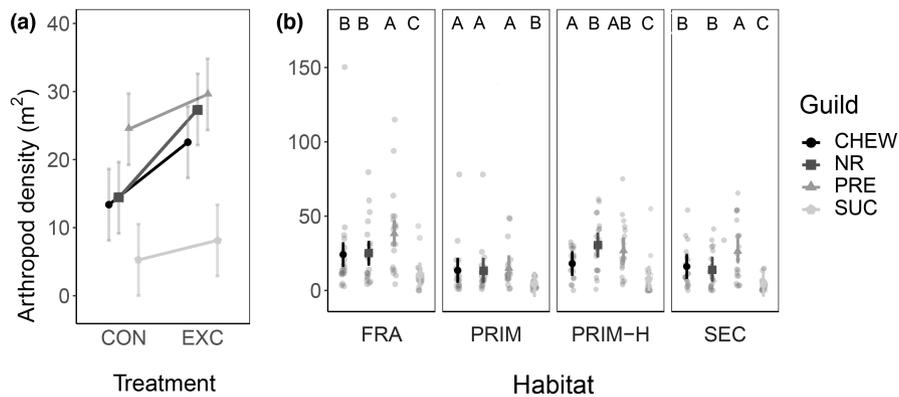


FIGURE 2 The effect of (a) treatment and (b) habitat on arthropod density (abundances per m² of foliage) for four feeding guilds. Each point represents observed value per sapling. Thick points and whiskers represent estimated marginal means and their 95 percent quantile. Significant pairwise comparisons were tested by Tuckey post hoc tests and in in case of habitat are indicated with letters. CHEW – leaf chewers, PRE – predatory arthropods (mesopredators), NR – other arthropods, SUC – sap suckers; CON – Control, EXC – Exclosure, FRA – primary forest fragment, PRIM – primary lowland forest, PRIM-H – primary montane forest, SEC – secondary forest

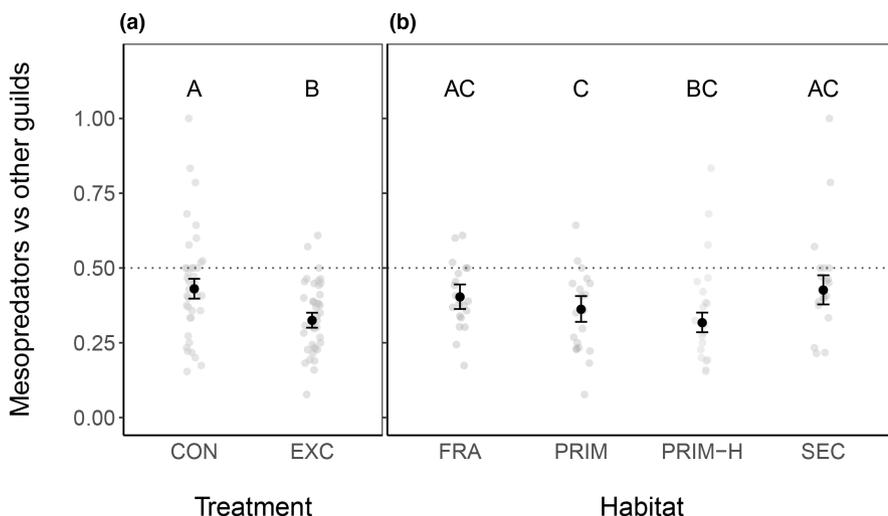


FIGURE 3 The effect of (a) treatment and (b) habitat on the mesopredator-other guilds' abundance ratio. Thick points and whiskers represent estimated marginal means and their 95 percent quantile. CON – control, EXC – exclosure, FRA – primary forest fragment, PRIM – primary lowland forest, PRIM-H – primary montane forest, SEC – secondary forest

(Figure 4a). Furthermore, there were general differences in body size for guilds across habitats (Kenward-Roger $F_9 = 17.13$, $p < .001$), which applied again only to leaf chewers and other arthropods and not for mesopredators and sap suckers. However, while leaf chewers were by 61–95% bigger in primary montane forest than in other habitats, other arthropods were by 69–104% smaller in primary montane forest than in other habitats (averaged across both treatments; Figure 4b). This pattern translated into the mesopredators-leaf chewers body size ratio, which was significantly lower in primary montane than in the other three habitats (Figure S8).

4 | DISCUSSION

Our study showed that insectivorous vertebrates can play an important role in top-down control processes in tropical forests in Papua New Guinea. In this three-month long study, they suppressed arthropod assemblages by ca. 51–63% and, consequently, overall herbivory by 41% (Figure 1). As expected, we confirmed that vertebrate predators provide an important ecosystem service in tropical forest understories, and even their short-term exclusion may lead to distortion in trophic cascades resulting in plant damage and potential consequences on forest productivity. Our results are in line with several studies that found support for the significant impacts of predators (Karp & Daily, 2014; Maas et al., 2013; Van Bael et al., 2007), whereas others reported a negligible effect of vertebrate insectivores on trophic cascades (Mooney & Linhart, 2006; Schwenk et al., 2010).

We suggest that vertebrate predators seem to be feeding preferentially on non-predatory arthropods, since the exclusion of

vertebrate predators led to a decrease in the abundance and mean body size ratios of mesopredators to other guilds (Figures 3 and S6), and mesopredators to leaf chewers (Figures S7 and S8). At the same time, there was basically no change detected in the control to exclosure ratio for separate mesopredator taxa, except in secondary lowland forest (Table S1), where ant densities increased in the exclosure. This is partially in contrast with another experimental studies from tropics, which showed a significant effect of birds on Lepidoptera larvae, Blattodea, and Araneae (Perfecto et al., 2004; Van Bael & Brawn, 2005). Further support for our conclusion that vertebrate predators feed preferentially on non-predatory arthropods is the observation that they caused a reduction in the overall mean body size of leaf chewers and arthropods with no relationship to herbivory, but they did not affect the body size of mesopredators (Figure 4a). Contrary to our hypothesis and the conclusions of several studies (Mooney et al., 2010; Philpott et al., 2004; Sam et al., 2014; Van Bael & Brawn, 2005), our results suggest a neutral or weak effect of intraguild predation caused by vertebrate predation on mesopredators (Table S1, Figure S8). Similarly to our study, size-based prey partitioning was observed in a temperate broad leaf forest in the USA (Singer et al., 2017).

Mesopredators were comprised of 69% Araneae (spiders), which have been observed making up a substantial proportion of bird diet in lower elevations in Papua New Guinea (Sam et al., 2017). Predatory arthropods are usually spiders or hymenopterans, which have naturally higher abundances and richness in lowland rather than in highland habitats (Lalisan et al., 2015). Indeed, Sam et al. (2022) recorded that exclusion of vertebrate insectivores strongly enhanced abundances of spiders at lower elevations but only mildly at higher

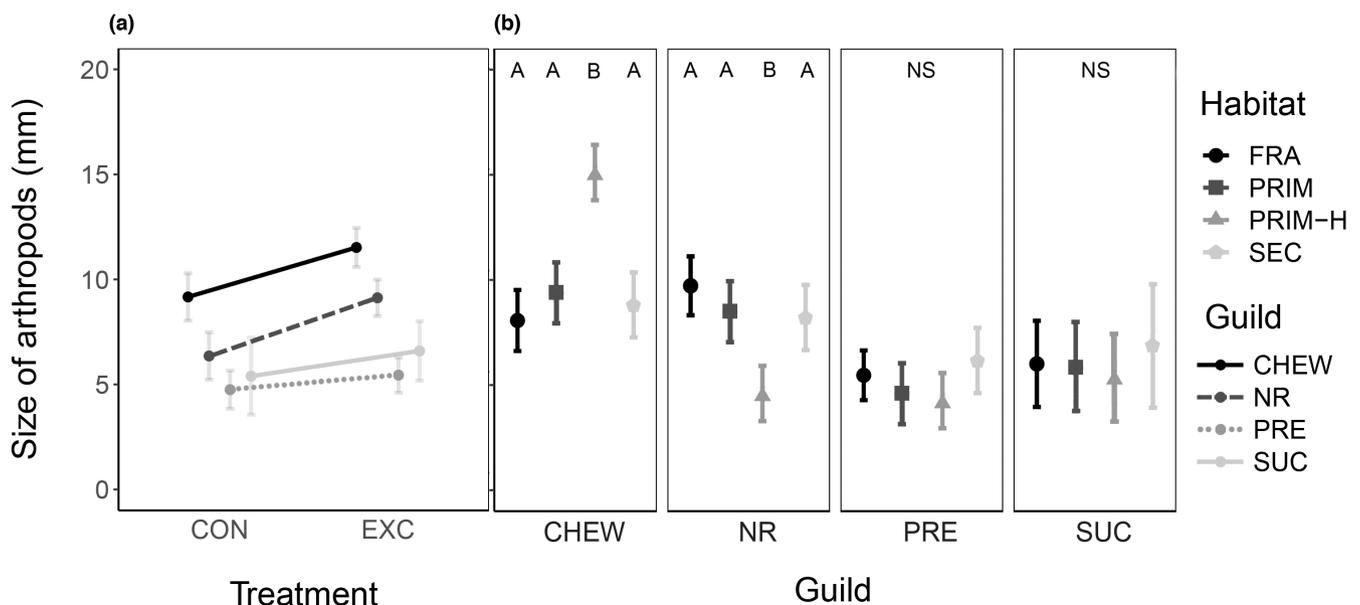


FIGURE 4 The effect of (a) treatment and (b) habitat on arthropod body size (mm) for four feeding guilds. Points and whiskers represent estimated marginal means and their 95 percent quantile. Significant pairwise comparisons were tested by Tuckey post hoc tests and in case of habitat are indicated with letters. CON - control, EXC - exclosure, FRA - primary forest fragment, PRIM - primary lowland forest, PRIM-H - primary montane forest, SEC - secondary forest. CHEW - leaf chewers, PRE - predatory arthropods (mesopredators), NR - other arthropods, SUC - sap suckers

elevations. It is surprising, therefore, that mesopredators were not able to expand to fill the “vacant” enemy-free space in the three trophic level cascades created by the exclusion of vertebrate predators in primary lowland forest.

Such a conundrum might be rooted in the fact that there may be multiple predator effects cascading down to plants, which may vary from additivity to antagonism in an ecologically dynamic manner (Finke & Denno, 2005; Singer et al., 2017). For example, top-down control by vertebrate predators may be buffered by intraguild predation within the mesopredator community (Finke & Denno, 2005). Hunting strategy (and/or diet specialization) in spider assemblages seems to determine whether spiders (i) partition prey resources with vertebrate predators and what prey or prey size will be most impacted by them; (ii) act as prey to vertebrate predators; (iii) are intraguild predators (Finke & Denno, 2005). Actively hunting spiders, for example, preferred to exploit prey which are 50–80% of their own body size and seem to be more affected by bird predation. In contrast, web-builders have a greater range of prey size and they are not directly affected by birds (Mooney & Linhart, 2006; Nentwig & Wissel, 1986).

In our results and in contrast to our expectations, habitat disturbance and elevation changed the direction of the effect of vertebrate predators on arthropod assemblages rather mildly and this translated into small differences in herbivore damage (Figure S5). Our results suggest that the expected diminution in the insectivorous bird assemblages in secondary forest and forest fragment observed by Sam et al. (2014) may not be sufficient to weaken the strength of the trophic cascades in our experiment, because we excluded also bats. The presence of bats may have counterbalanced the predicted weaker top-down effect caused by degraded bird communities in the forest fragment and the secondary forest, as they display similar predatory potential as birds (Morrison & Lindell, 2012). In contrast to birds, bat responses to habitat changes are highly idiosyncratic (Meyer et al., 2016). Insectivorous bat assemblages usually respond to factors such as the presence of water bodies and distance from urban areas in terms of species composition and foraging strategies (Meyer et al., 2016). However, little is known about insectivorous bat assemblages in Papua New Guinea (Sivault et al., 2022). Our results are further supported by study by Tvardikova and Novotny (2012) who observed a significantly higher bird attack rate on exposed artificial caterpillars on saplings in primary montane forest compared with lowland forests (primary, fragment and secondary) in Papua New Guinea. However, although our study detected overall significant effects of top-down control by vertebrate predators, we should not rule out the possibility that a longer-term experiment could yield stronger differences in trophic cascades across different tropical forest habitats (but see Eveleigh et al., 2001). Indeed, a recent review showed that the densities of mesopredators after predator exclusion are dependent on the duration of enclosure, and mesopredators only started to exploit the “vacant” enemy-free space after ca. 3 months (Sam et al., 2022). The manner in which vertebrate insectivores and associated ecological functions

respond to disturbance in forested landscapes, however, warrants further investigation.

In addition to shedding light on the general mechanisms affecting terrestrial trophic cascades between vertebrate predators and plants, our results point out the complexity of these interactions across different tropical forest habitats, which should be appropriately addressed in future studies. The prey and mesopredator species are affected on multiple levels by resource competition, apparent competition, intraguild predation and prey partitioning (Chase et al., 2002; Finke & Denno, 2005; Singer et al., 2017). It is crucial, therefore, that new studies consider not only abundances, body sizes in context of whole communities (Borkhataria et al., 2006), but also their ecological strategies (Gunnarsson, 2007), such as hunting modes (Nentwig & Wissel, 1986), diet specialization (Piñol et al., 2010), and defense strategies (Tvardikova & Novotny, 2012). In addition, plant traits and defenses may have bottom-up effects on arthropod assemblages (Sam et al., 2020; Volf et al., 2020).

Accordingly, future studies should focus on the appropriate standardization of herbivory rates, so as to be comparable with other studies. Our observed herbivory values, for example, were around 6.2% (emmean in control) and 8.8% (emmean in enclosure), which is substantially different from estimates in some previous studies from Papua New Guinea (e.g., Plowman et al., 2017 estimated 20%–40% damage per individual leaf, but see Sam et al., 2020, who measured mean herbivory as 2.4% on average). Such substantial differences might reflect the computational approaches taken. Herbivory percentage per single leaf or single leaf frame tends to increase the herbivory value per sapling because it neglects the actual size of the leaf area consumed and there may be a large variation in estimated consumed area (Kozlov et al., 2014). So, not only should the consumed leaf area not be roughly estimated as was pointed out by Kozlov et al. (2014), Zvereva and Kozlov (2014) and Sam et al. (2020), but we also suggest computing the herbivory percentage as $(\text{total leaf area consumed})/(\text{total [reconstructed] leaf area}) * 100$, which does not neglect the actual leaf area consumed.

In conclusion, the exclusion of vertebrate predators resulted in an increase of the overall density of arthropods by 51–62%. Our results, however, indicate stronger effects of vertebrate predators on leaf chewers and non-herbivorous arthropods than on mesopredators. Similarly, the exclusion of vertebrate predators had no effect on the body size of predators and sap suckers but increased the body size of leaf chewers by 26% and of other arthropods by 47%. This three-month experimental exposure to larger arthropods and increased arthropod densities caused an ~41% increase in herbivorous damage to plants. Contrary to our expectations, we detected only small differences in the strength of the trophic cascades among study habitats, suggesting that variability among the habitats had a stronger predictive value, than the potential differences in top-down effects of vertebrate predator assemblages. Finally, we highlight the necessity for further studies using our approach, in order to drill down into the mechanisms and processes that mold food web structure in tropical forests.

ACKNOWLEDGMENTS

We thank all the assistants and parataxonomists from the Binatang Research Centre for their help with logistics and permits. Landowners of Kotet, Wanang and Baiteta kindly allowed access to their land and provided assistance in the field. Martin Mogia helped to identify the collected insects and oversaw the experiment in Kotet. Anna Mrazova and David Mendez Diez provided valuable comments on the manuscript. We further thank to Roger Kitching and Phillip Butterill, who proofread our manuscript.

FUNDING INFORMATION

This work was financially supported by Czech Grant Agency of Czech Republic (18-23794Y) and by European Research Council Starting Grant BABE 805189.

CONFLICT OF INTEREST

The author(s) declare they have no competing interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.8931zcrtr> (Tahadlova et al., 2022).

ORCID

Marketa Houska Tahadlova  <https://orcid.org/0000-0003-2985-2963>

Ondrej Mottl  <https://orcid.org/0000-0002-9796-5081>

Katerina Sam  <https://orcid.org/0000-0002-3436-0579>

REFERENCES

- Atlegrim, O. (1989). Exclusion of birds from bilberry stands: Impact on insect larval density and damage to the bilberry. *Oecologia*, 79, 136–139.
- Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506, 85–88. <https://doi.org/10.1038/nature12911>
- Barton, K. (2022). MuMIn: Multi-Model Inference. R package version 1.46.0. <https://CRAN.R-project.org/package=MuMIn>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Belovsky, G. E., & Slade, J. B. (1993). The role of vertebrate and invertebrate predators in a grasshopper community. *Oikos*, 68, 193–201.
- Bolker, B., & R Development Core Team. (2020). bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.23.1. <https://CRAN.R-project.org/package=bbmle>
- Borkhataria, R. R., Collazo, J. A., & Groom, M. J. (2006). Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecological Applications*, 16, 696–703. [https://doi.org/10.1890/1051-0761\(2006\)016\[0696:AEVPO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0696:AEVPO]2.0.CO;2)
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). Modeling zero-inflated count data with glmmTMB. *bioRxiv*, 1–14. <https://doi.org/10.1101/132753>
- Cardinale, B. J., Harvey, C. T., Gross, K., & Ives, A. R. (2003). Biodiversity and biocontrol: Emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters*, 6, 857–865. <https://doi.org/10.1046/j.1461-0248.2003.00508.x>
- Cassano, C. R., Silva, R. M., Mariano-Neto, E., Schroth, G., & Faria, D. (2016). Bat and bird exclusion but not shade cover influence arthropod abundance and cocoa leaf consumption in agroforestry landscape in Northeast Brazil. *Agriculture, Ecosystems and Environment*, 232, 247–253. <https://doi.org/10.1016/j.agee.2016.08.013>
- Chan, A. A. Q., & Banks-Leite, C. (2020). Habitat modification mediates the strength of trophic cascades on oak trees. *Perspectives in Ecology and Conservation*, 4, 313–318. <https://doi.org/10.1016/j.pecon.2020.09.002>
- Chase, J. M., Abrams, P. A., Grover, J. P., Diehl, S., Chesson, P., Holt, R. D., Richards, S. A., Nisbet, R. M., & Case, T. J. (2002). The interaction between predation and competition: A review and synthesis. *Ecology Letters*, 5, 302–315. <https://doi.org/10.1046/j.1461-0248.2002.00315.x>
- Coley, P. D., & Barone, J. A. (1996). Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, 27, 305–335.
- Eveleigh, N. C. P., Majer, J. D., & Recher, H. F. (2001). The effects of reducing bird predation on canopy arthropods of marri (*Eucalyptus calophylla*) saplings on the swan coastal plain, Western Australia. *Journal of the Royal Society of Western Australia*, 84, 13–21.
- Fáveri, S. B., Vasconcelos, H. L., & Dirzo, R. (2008). Effects of Amazonian forest fragmentation on the interaction between plants, insect herbivores, and their natural enemies. *Journal of Tropical Ecology*, 24, 57–64. <https://doi.org/10.1017/S0266467407004592>
- Finke, D. L., & Denno, R. F. (2003). Intra-guild predation relaxes natural enemy impacts on herbivore populations. *Ecological Entomology*, 28, 67–73. <https://doi.org/10.1046/j.1365-2311.2003.00475.x>
- Finke, D. L., & Denno, R. F. (2005). Predator diversity and the functioning of ecosystems: The role of intraguild predation in dampening trophic cascades. *Ecology Letters*, 8, 1299–1306. <https://doi.org/10.1111/j.1461-0248.2005.00832.x>
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478, 378–381. <https://doi.org/10.1038/nature10425>
- Greenberg, R., Bichier, P., Angon, A. C., MacVean, C., Perez, R., & Cano, E. (2000). The impact of avian insectivory on arthropods and leaf damage in some Guatemalan coffee plantations. *Ecology*, 81, 1750–1755. <https://doi.org/10.2307/177321>
- Gruner, D. S. (2004). Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology*, 85, 3010–3022.
- Gunnarsson, B. (2007). Bird predation on spiders: Ecological mechanisms and evolutionary consequences. *The Journal of Arachnology*, 35, 509–529. <https://doi.org/10.1636/RT07-64.1>
- Halaj, J., & Wise, D. H. (2001). Terrestrial trophic cascades: How much do they trickle? *The American Naturalist*, 157, 262–281. <https://doi.org/10.1086/319190>
- Ives, A. R., Cardinale, B. J., & Snyder, W. E. (2005). A synthesis of sub-disciplines: Predator-prey interactions, and biodiversity and ecosystem functioning. *Ecology Letters*, 8, 102–116. <https://doi.org/10.1111/j.1461-0248.2004.00698.x>
- Kalka, M. B., Smith, A. R., & Kalko, E. K. V. (2008). Bats limit arthropods and herbivory in a tropical Forest. *Science*, 320, 71. <https://doi.org/10.1126/science.1153352>
- Karp, D. S., & Daily, G. C. (2014). Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology*, 95, 1065–1074. <https://doi.org/10.1890/13-1012.1>
- Kozlov, M. V., Zverev, V., & Zvereva, E. L. (2014). Confirmation bias leads to overestimation of losses of woody plant foliage to insect herbivores in tropical regions. *PeerJ*, 2, 709. <https://doi.org/10.7717/peerj.709>

- Lalisan, J. A., Dupo, A. L. B., & Nuneza, O. (2015). Diversity of spiders along an elevational gradient in Mt. Pinukis, Zamboanga del Sur, Philippines. *Journal of Biodiversity and Environmental Sciences*, 7, 190–201. <https://doi.org/10.31396/Biodiv.Jour.2020.11.2.593.610>
- Lenth, R. V. (2020). emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://cran.r-project.org/web/packages/emmeans/index.html>. Accessed 30 January 2021.
- Losey, J. E., & Denno, R. F. (1998). Positive predator–predator interactions: Enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.
- Lüdecke, D., Makowski, D., Waggoner, P., & Patil, I. (2020). performance: Assessment of Regression Models Performance. <https://easystats.github.io/performance/>. Accessed 30 March 2021.
- Maas, B., Clough, Y., & Tscharnke, T. (2013). Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters*, 16, 1480–1487. <https://doi.org/10.1111/ele.12194>
- Maas, B., Heath, S., Grass, I., Cassano, C., Classen, A., Faria, D., Gras, P., Williams-Guillén, K., Johnson, M., Karp, D. S., & Linden, V. (2019). Experimental field enclosure of birds and bats in agricultural systems—Methodological insights, potential improvements, and cost-benefit trade-offs. *Basic and Applied Ecology*, 35, 1–12. <https://doi.org/10.1016/j.baae.2018.12.002>
- Mäntylä, E., Klemola, T., & Laaksonen, T. (2011). Birds help plants: A meta-analysis of top-down trophic cascades caused by avian predators. *Oecologia*, 165, 143–151. <https://doi.org/10.1007/s00442-010-1774-2>
- Marquis, R. J., & Whelan, C. (1996). Plant morphology and recruitment of the third trophic level: Subtle and little-recognized defenses? *Oikos*, 75, 330.
- Mazia, C. N., Chaneton, E. J., Kitzberger, T., & Garibaldi, L. A. (2009). Variable strength of top-down effects in *Nothofagus* forests: Bird predation and insect herbivory during an ENSO event. *Austral Ecology*, 34, 359–367. <https://doi.org/10.1111/j.1442-9993.2009.01933.x>
- Meyer, C. F. J., Struebig, M. J., & Willig, M. R. (2016). Responses of tropical bats to habitat fragmentation, logging, and deforestation. In C. C. Voigt & T. Kingston (Eds.), *Bats in the anthropocene: Conservation of bats in a changing world* (pp. 63–103). Springer International Publishing. https://doi.org/10.1007/978-3-319-25220-9_4
- Mooney, K. (2007). Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology*, 88, 2005–2014. <https://doi.org/10.1890/0012-9658>
- Mooney, K. A., Gruner, D. S., Barber, N. A., Van Bael, S. A., Philpott, S. M., & Greenberg, R. (2010). Interactions among predators and the cascading effects of vertebrate insectivores on arthropod communities and plants. *Proceedings of the National Academy of Sciences of the United States of America*, 107, 7335–7340. <https://doi.org/10.1073/pnas.1001934107>
- Mooney, K. A., & Linhart, Y. B. (2006). Contrasting cascades: Insectivorous birds increase pine but not parasitic mistletoe growth. *Journal of Animal Ecology*, 75(2), 350–357. <https://doi.org/10.1111/j.1365-2656.2006.01054.x>
- Morrison, E. B., & Lindell, C. A. (2012). Birds and bats reduce insect biomass and leaf damage in tropical forest restoration sites. *Ecological Applications*, 22, 1526–1534. <https://doi.org/10.1890/11-1118.1>
- Nentwig, W., & Wissel, C. (1986). A comparison of prey lengths among spiders. *Oecologia*, 68, 595–600.
- Novotny, V., Miller, S. E., Baje, L., Balagawi, S., Basset, Y., Cizek, L., Craft, K. J., Dem, F., Drew, R. A. I., Hulcr, J., Leps, J., Lewis, O. T., Pokon, R., Stewart, A. J. A., Samuelson, G. A., & Weiblen, G. D. (2010). Guild-specific patterns of species richness and host specialization in plant – herbivore food webs from a tropical forest. *The Journal of Animal Ecology*, 79, 1193–1203. <https://doi.org/10.1111/j.1365-2656.2010.01728.x>
- Oksanen, L., Fretwell, S. D., Arruda, J., & Niemelä, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, 118, 240–262.
- Paquette, A., & Hargreaves, A. L. (2021). Biotic interactions are more important at species' warm vs. cool range-edges: A synthesis. *Ecology Letters*, 24(11), 2427–2438. <https://doi.org/10.1111/ele.13864>
- Perfecto, I., Vandermeer, J. H., Bautista, G. L., Nunez, G. I., Greenberg, R., Bichier, P., & Langridge, S. (2004). Greater predation in shaded coffee farms: The role of resident neotropical birds. *Ecology*, 85, 2677–2681.
- Philpott, S. M., Greenberg, R., Bichier, P., & Perfecto, I. (2004). Impacts of major predators on tropical agroforest arthropods: Comparisons within and across taxa. *Oecologia*, 140, 140–149. <https://doi.org/10.1007/s00442-004-1561-z>
- Philpott, S. M., Soong, O., Lowenstein, J. H., Pulido, A. L., Lopez, D. T., Flynn, D. F., & DeClerck, F. (2009). Functional richness and ecosystem services: Bird predation on arthropods in tropical agroecosystems. *Ecological Applications*, 19, 1858–1867. <https://doi.org/10.1890/08-1928.1>
- Piñol, J., Espadaler, X., Cañellas, N., Martínez-Vilalta, J., Barrientos, J. A., & Sol, D. (2010). Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove. *Ecological Entomology*, 35, 367–376. <https://doi.org/10.1111/j.1365-2311.2010.01190.x>
- Plowman, N. S., Hood, A. S., Moses, J., Redmond, C., Novotny, V., Klimes, P., & Fayle, T. M. J. P. R. S. B. (2017). Network reorganization and breakdown of an ant–plant protection mutualism with elevation. *Proceedings of the Royal Society of Biological Sciences*, 284, 20162564. <https://doi.org/10.1098/rspb.2016.2564>
- Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20, 297–330.
- Preisser, E. (2008). Trophic structure. *Encyclopedia of Ecology*, 1, 3608–3616. ISBN 9780080454054. [doi:10.1016/b978-0-08045405-4.00558](https://doi.org/10.1016/b978-0-08045405-4.00558)
- Roels, S. M., Porter, J. L., & Lindell, C. A. (2018). Predation pressure by birds and arthropods on herbivorous insects affected by tropical forest restoration strategy. *Restoration Ecology*, 26, 1203–1211. <https://doi.org/10.1111/rec.12693>
- Romero, G., Gonçalves-Souza, T., Roslin, T., Marquis, R., Marino, N., Novotny, V., Cornelissen, T., Orivel, J., Sui, S., & Aires, G. (2021). Climate variability and aridity modulate the role of leaf shelters for arthropods: A global experiment. *Global Change Biology*, 27, 3694–3710. <https://doi.org/10.1111/gcb.16150>
- Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., Barrio, I. C., Basset, Y., Boesing, A. L., Bonebrake, T. C., Cameron, E. K., Dáttilo, W., Donoso, D. A., Drozd, P., Gray, C. L., Hik, D. S., Hill, S. J., Hopkins, T., Huang, S., ... Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. *Science*, 356, 742–744. <https://doi.org/10.1126/science.aaj1631>
- Sam, K., Houska Tahadlova, M., Mrazova, A., Freiberger, I., Toszogyova, A., & Sreekar, R. (2022). The impact of ants and vertebrate predators on arthropods and plants: a meta-analysis. *bioRxiv*. <https://doi.org/10.1101/2022.06.29.498005>
- Sam, K., & Koane, B. (2020). Biomass, abundances, and abundance and geographical range size relationship of birds along a rainforest elevational gradient in Papua New Guinea. *PeerJ*, 8, e9727. <https://doi.org/10.7717/peerj.9727>
- Sam, K., Koane, B., Jeppy, S., & Novotny, V. (2014). Effect of forest fragmentation on bird species richness in Papua New Guinea. *Journal of Field Ornithology*, 85, 152–167. <https://doi.org/10.1111/jof.12057>
- Sam, K., Koane, B., Jeppy, S., Sykorova, J., & Novotny, V. (2017). Diet of land birds along an elevational gradient in Papua New Guinea. *Scientific Reports*, 7, 1–10. <https://doi.org/10.1038/srep44018>
- Sam, K., Koane, B., & Novotny, V. (2015). Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. *Ecography*, 38, 293–300. <https://doi.org/10.1111/ecog.00979>
- Sam, K., Koane, B., Sam, L., Mrazova, A., Segar, S., Volf, M., Moos, M., Simek, P., Sisol, M., & Novotny, V. (2020). Insect herbivory and

- herbivores of *Ficus* species along a rain forest elevational gradient in Papua New Guinea. *Biotropica*, 1–14, 263–276. <https://doi.org/10.1111/btp.12741>
- Sanz, J. J. (2001). Experimentally increased insectivorous bird density results in a reduction of caterpillar density and leaf damage to Pyrenean oak. *Ecological Research*, 16, 387–394. <https://doi.org/10.1046/j.1440-1703.2001.00403.x>
- Schwenk, W. S., Strong, A. M., & Sillett, T. S. (2010). Effects of bird predation on arthropod abundance and tree growth across an elevational gradient. *Journal of Avian Biology*, 4, 367–377. <https://doi.org/10.1111/j.1600-048X.2009.04963.x>
- Sekercioglu, C. H. (2006). Increasing awareness of avian ecological function. *Trends in Ecology and Evolution*, 21, 464–471. <https://doi.org/10.1016/j.tree.2006.05.007>
- Singer, M. S., Clark, R. E., Lichter-Marck, I. H., Johnson, E. R., & Mooney, K. A. (2017). Predatory birds and ants partition caterpillar prey by body size and diet breadth. *The Journal of Animal Ecology*, 86, 1363–1371. <https://doi.org/10.1111/1365-2656.12727>
- Sivault, E., Amick, P. K., Armstrong, K. N., Novotny, V., & Sam, K. (2022). Species richness and community structure of bats along a forest elevational transect in Papua New Guinea. *bioRxiv*. <https://doi.org/10.1101/2022.02.17.480839>
- Snyder, W. E., & Ives, A. R. (2003). Interactions between specialist and generalist natural enemies: Parasitoids, predators, and pea aphid biocontrol. *Ecology*, 84, 91–107. [https://doi.org/10.1890/0012-9658\(2003\)084\[0091:IBSAGN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0091:IBSAGN]2.0.CO;2)
- Straub, C. S., & Snyder, W. E. (2006). Species identity dominates the relationship between predator biodiversity and herbivore suppression. *Ecology*, 87, 277–282. <https://doi.org/10.1890/05-0599>
- Tahadlova, M. H., Mottl, O., Jorge, L. R., Koane, B., Novotny, V., & Sam, K. (2022). Data from: Trophic cascades in tropical rainforests: Effects of vertebrate predator exclusion on arthropods and plants in Papua New Guinea. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.8931zcrtr>
- Team R Core. (2021). *R: A language and environment for statistical computing*. Team R Core.
- Terborgh, J. W. (2015). Toward a trophic theory of species diversity. *Proceedings of the National Academy of Sciences of The United States of America*, 112, 11415–11422. <https://doi.org/10.1073/pnas.1501070112>
- Tvardikova, K., & Novotny, V. (2012). Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. *The Journal of Tropical Ecology*, 28, 331–341. <https://doi.org/10.1017/S0266467412000235>
- Van Bael, S. A., Bichier, P., & Greenberg, R. (2007). Bird predation on insects reduces damage to the foliage of cocoa trees (*Theobroma cacao*) in western Panama. *Journal of Tropical Ecology*, 23(6), 715–719. <https://doi.org/10.1017/S0266467407004440>
- Van Bael, S. A., & Brawn, J. D. (2005). Erratum: The direct and indirect effects of insectivory by birds in two contrasting Neotropical forests (*Oecologia* (2005) 143 (106-166) DOI: 10.007/s00442-004-1774-1). *Oecologia*, 145, 658–668.
- Van Bael, S. A., Brawn, J. D., & Robinson, S. K. (2003). Birds defend trees from herbivores in a Neotropical forest canopy. *Proceedings of the National Academy of Sciences of The United States of America*, 100, 8304–8307. <https://doi.org/10.1073/pnas.1431621100>
- Vance-Chalcraft, H. D., Rosenheim, J. A., Vonesh, J. R., Osenberg, C. W., & Sih, A. (2007). The influence of intraguild predation on prey suppression and prey release: A meta-analysis. *Ecology*, 88, 2689–2696. <https://doi.org/10.1890/06-1869.1>
- Volf, M., Laitila, J. E., Kim, J., Sam, L., Sam, K., Isua, B., Sisol, M., Wardhaugh, C. W., Vejmelka, F., Miller, S. E., Weiblen, G. D., Salminen, J. P., Novotny, V., & Segar, S. T. (2020). Compound specific trends of chemical Defences in *Ficus* along an elevational gradient reflect a complex selective landscape. *Journal of Chemical Ecology*, 46(4), 442–454. <https://doi.org/10.1007/s10886-020-01173-7>
- Wright, S. J. (2002). Plant diversity in tropical forests: A review of mechanisms of species coexistence. *Oecologia*, 130(1), 1–14. <https://doi.org/10.1007/s004420100809>
- Zvereva, E. L., Castagneyrol, B., Cornelissen, T., Forsman, A., Hernández-Agüero, J. A., Klemola, T., Paolucci, L., Polo, V., Salinas, N., & Theron, K. J. (2019). Opposite latitudinal patterns for bird and arthropod predation revealed in experiments with differently colored artificial prey. *Ecology and Evolution*, 9, 14273–14285. <https://doi.org/10.1002/ece3.5862>
- Zvereva, E. L., & Kozlov, M. V. (2014). Effects of herbivory on leaf life span in woody plants: A meta-analysis. *Journal of Ecology*, 102, 873–881. <https://doi.org/10.1111/1365-2745.12252>

SUPPORTING INFORMATION

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

How to cite this article: Houska Tahadlova, M., Mottl, O., Jorge, L. R., Koane, B., Novotny, V., & Sam, K. (2022). Trophic cascades in tropical rainforests: Effects of vertebrate predator exclusion on arthropods and plants in Papua New Guinea. *Biotropica*, 00, 1–11. <https://doi.org/10.1111/btp.13160>