Vertebrates but not ants protect rainforest trees from herbivorous insects along an elevational gradient in Papua New Guinea

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Abstract

The theory on trophic interactions between plants, insect herbivores and their predators predict that predators increase plant biomass by feeding on herbivores. However, it remains unclear whether different types of predators regulate herbivores to the same degree, and how the trophic interactions affect lower trophic levels along elevational gradients, where predator communities differ significantly. In the present study, we investigated the impact of vertebrate predators and ants (individually and in combinations) on arthropod communities and on leaf herbivory, along a complete tropical forest gradient in Papua New Guinea. In two six-month long predator exclusion experiments representing wet and dry season, we excluded predators from 560 saplings growing at 8 study sites, evenly spaced at 500 m elevational increments from 200 to 3700m a.s.l. We found the density of arthropods to increase significantly by 37% on average when the vertebrate predators were removed and by 33% when both ants and vertebrates were removed. This effect was further significantly affected both by season and elevation. At lower trophic level, exclusion of vertebrates and vertebrates and ants led to a significant increase in leaf damage by 50 and 36% respectively. In contrast, exclusion of ants alone had no significant effect neither on arthropod density not on leaf damage, which increased by 12% and 9% respectively. Our results further imply that relative contribution of birds and bats differs at various elevational sites, despite the effect of vertebrate predators remains to be robust along the whole elevational gradient. In contrast, trophic cascades caused by ants translated into increased herbivory only at the most productive sites of the elevational gradient, where the abundances of ants are also the highest. Our results indicate that disappearance of insectivorous vertebrate predators would have significantly negative consequences for plants.

Introduction

Insect herbivores are the major consumers of plant leaf tissue in tropical forest (Coley and Aide 1991, Coley and Barone 1996, but Suzuki, et al. 2013), and their impact is much increased in the absence of top-down control (Mooney, et al. 2010, Sam, et al. 2022). The top-down control of insect densities by insectivorous predators is therefore a highly valued ecological service in a range of tropical ecosystems (Schmitz 2006, Sekercioglu 2006). However, disparate insectivorous predator groups are usually assumed to have similar effects and are thus treated as a single functional unit. Therefore, their individual effects remain mostly unknown. In many natural ecosystems, several groups of predators affect the arthropod herbivores jointly (Mooney 2007, Perfecto and Vandermeer 1996, Richards and Coley 2007, Sih, et al. 1998). The often-complex trophic dynamics of multiple types of predators in the same community and their cascading effect on plant performance remain an unresolved and important challenge in ecology (Singer, et al. 2017). This is mainly because the strength of trophic cascades between predators, prey and plants has been found to be quite variable both within (Moon and Stiling 2004, Mooney and Linhart 2006) and between communities (Shurin, et al. 2002).

Insectivorous vertebrates, bats, and birds more specifically, consume large quantities of insects and other arthropods (Kalka and Kalko 2006, Mooney, et al. 2010, Nyffeler, et al. 2018). They are both likely to act as intraguild predators, feeding both on predatory as well as herbivore arthropods (Ingala, et al. 2021, Karp and Daily 2014, Milne, et al. 2016, Sam, et al. 2017). The impact of ubiquitous insectivorous birds on lower trophic levels was shown in some, but not all, studies where their predation has been assessed (Mooney, et al. 2010, Van Bael, et al. 2008). Bat impact on arthropods and herbivory might be comparable to the effect of birds according to some studies (Kalka and Kalko 2006, Williams-Guillén, et al. 2008). Yet, it was considered as negligible in many other studies, to the extent that the combined effect of birds and bats was measured but reported as the effect of birds (Mooney, et al. 2010, Sam, et al. 2022). Unfortunately, the most common methodological approach to studying trophic cascades, i.e., covering the foliage by netting, preventing the access of predators, and measuring the effect of the top-down control, quantifies only combined effect of birds and bats (Greenberg, et al. 2000, Holmes, et al. 1979, Van Bael, et al. 2003, but see Kalka, et al. 2008).

Ants are recognised as other important predators in many habitats (Hölldobler and Wilson 1990). Despite having been studied as natural enemies and biological control agents (Mestre, et al. 2012, Philpott and Armbrecht 2006, Way and Khoo 1992), their importance as predators remains equivocal. In many studies, their effect on lower trophic levels was not detected or was not consistent in time (Tanhuanpää, et al. 2001, Sam, et al. 2022). Plant damage in the absence of ants

was reported to increase between 0 and 250% on average and it was significantly dependent on the duration of the ant exclosure, as well as on the productivity of the study site (Sam, et al. 2022). Ant exclosures are difficult to conduct (Hood, et al. 2022) thus bait removal is often considered as a proxy of predation (e.g., Liu, et al. 2020, Roslin, et al. 2017, Burger, et al. 2021). Unfortunately, this method may not measure accurately the realized top-down control and trophic cascade to plants by ants.

Change in the diversity and abundance of different animal taxa, including predators, along elevational gradients are one of the most striking biogeographic patterns on Earth (Colwell, et al. 2016, McCain 2005, Rahbek 1995, Sam, et al. 2019). Differences in distribution along the same gradient create sites where groups of predators might have different relative importance. As such, elevational gradients provide an excellent experimental environment for studies focused on individual and combined effects of insectivorous predators on prey and plants (Schemske, et al. 2009). Further, potential shifts in distribution of taxa due to climate change might lead to significant changes in the combined effect of predators on lower trophic levels (Chen, et al. 2011). Therefore, it is increasingly important to understand individual and combined effects of various groups of predators along large environmental gradients.

Changes in diversity along elevational gradients are accompanied also with changes in body size, with lowland animals being in general larger than animals at higher elevational sites. Besides that, differently sized predators feed on prey of different sizes and we can thus expect their effect to be detectable also in the mean body size of insect communities. For example, birds were shown to reduce the mean size of caterpillars by 12% by feeding on large individuals (Singer, et al. 2017). Similarly, birds and bats reduced mean body size of Araneae, Formicidae and arthropod larvae (Karp and Daily 2014). In contrast to vertebrate predators, ants are expected to hunt on smaller prey, thus their absence from an ecosystem might lead to increase of mean body size of arthropods.

In the present study, we investigated the impact of vertebrate predators and ants (individually and in combinations) on arthropod communities and on leaf herbivory, along a complete tropical forest gradient in Papua New Guinea. Specifically, we aimed to answer the following questions: (1) Do predators significantly affect the density of arthropods in various tropical habitats along the elevational gradient? We hypothesised, that removal of vertebrate predators, but not ants, will result in an increased density of arthropods on plants. (2) Does the potential effect of predators cascade down to the trophic level of plants and is it detectable on plant herbivory? Considering our first hypothesis, we expected that removal of vertebrate predators, but not ants, will have a measurable effect on plants and will result into increased herbivory. (3) Does any of the predator groups reduce the abundance of predatory arthropods in a different rat then the herbivore

arthropods? Intraguild predation, i.e., feeding on herbivorous and predatory arthropods in equal proportion, is expected to diminish the trophic cascades. We expected that both focal predator groups (i.e., vertebrate predators and ants) act as intraguild predators, diminishing the effect of the trophic cascade but not so much as it wouldn't be detectable. (4) Is the effect of ants and vertebrate predators independent of each other or do they interact? We hypothesised that the effect will be mostly independent and additive, as ants and vertebrate predators feed on different prey items and birds (and presumably also bats) do not consume many ants (Sam et al. 2017). (5) Is the effect of ants and vertebrate predators detectable on the mean body size of arthropod communities? We expected the arthropods to be relatively larger in absence of vertebrate predators and relatively bigger in absence of ants.

Materials and methods

Study sites and experimental trees

Our study was performed along the slopes of Mt. Wilhelm (4,509 m a.s.l.) in the Central Range of Papua New Guinea (Figure S1). The rainforest gradient spans from the lowland floodplains of the Ramu river (200 m a.s.l., 5° 44' S 145° 20' E) to the timberline (3,700 m a.s.l., 5° 47' S 145° 03' E). The gradient is 30 km long and consists of eight sites, evenly spaced at 500 m elevational increments. Average annual precipitation is 3,288 mm (local meteorological station) in the lowlands, rising to 4,400 mm at 3,700 m a.s.l., with a distinct condensation zone around 2500 – 2700 m a.s.l. Mean annual temperature (measured by our data loggers - (Sam, et al. 2019) decreases from 27.4°C at the lowland site to 8.4°C at the tree line at a constant rate of 0.54°C per 100 elevational metres. The habitats and zonation of forest types are described elsewhere (McAlpine, et al. 1983, Paijmans 1976, Sam, et al. 2019, Tvardikova 2013).

Prior to the experiment, we selected and tagged saplings belonging to 3 – 7 tree species at each elevational study site (Table S1). Unfortunately, no single tree species or genus is distributed along the complete elevational gradient. Therefore, we aimed to work with several *Ficus* species which represent the most dominant and ecologically important genus from 200 up to 2700 m a.s.l. At the highest two elevations, we had to work with other locally dominant species (Table S1). In total, we selected 80 (or 40 at 3,200 and 3,700m asl) individual saplings per each elevational site, i.e., 560 saplings along the elevational gradient for the whole project (Table S2). For statistical non-independence, we allowed at least 50 m between any pair of tree individuals. We visually assessed saplings of the focal species and selected individuals which had approximately 500 leaves growing within a well-developed crown 2.5 – 4 m above the ground, did not have any ant nests, and did not have any abnormally high herbivory or fungal damage. The selected tree species also did not

produce any exudates or sugar droplets attracting ants. Average leaf-sizes of the selected species ranged from 16.31 to 154.10 cm^2 (mean ± S.E. = 52.16 ± 6.12). Mean sapling DBH at the beginning of the experiment was 1.16 cm for exclosures and 1.17 cm for controls.

Experimental design

At elevational sites between 200 and 2,700 m a.s.l., we prevented access of vertebrate predators (i.e., birds and bats together, VER) to 20 out of the 80 preselected saplings at each elevational site. We also prevented access of ants to another 20 saplings (ANT) and finally we prevented access of both vertebrate predators and ants to another 20 saplings (ALL) at each elevation. We left 20 saplings without predator protection as controls (CON). At elevational sites 3,200 and 3,700 m, we protected 20 saplings against vertebrates (VER) and kept 20 as control saplings (CON). Ants naturally do not occur at these elevations (Moses 2015, Colwell et al. 2016), therefore there was no need to manipulate their absence.

Vertebrate (VER) exclosures were constructed from PVC tubes (1 cm in diameter) joined together by PVC corners and covered with agricultural nylon netting (mesh opening 3 x 3 cm, transparent green). Each exclosure had dimensions 2 x 2 x 2.5 m and comprised a volume of 10 m^3, which enclosed an average of 1.63 (± S.D. 1.02) m^2 of leaf area. The mesh size was comparable to other exclosure studies [e.g., 29×29 mm in Greenberg, et al. (2000); 25×25 mm in Mols and Visser (2002); 20×20 mm in Van Bael, et al. (2003)]. The exclosure materials did not attract arthropods, did not damage leaves or branches, and did not significantly reduce light. A system of ropes attached to neighbouring vegetation (i.e., strong branches) was used to hold the exclosures securely in place (not disturbing the foliage of the saplings by movements). Our observations confirmed that netting did not prevent the access of small lizards, as they were observed to crawl under the cage. However, one ca. 50 cm long lizard was found tangled in the netting and released, meaning the exclosures partially prevented access of non-flying insectivores which were not quantified in the study.

To exclude ants (ANT), we used the adhesive Tanglefoot® pest barrier (Philpott, et al. 2008, Philpott, et al. 2004) which we applied in a 30cm wide stripe around the trunk of the sapling at breast height. We removed all lianas and branches touching the sapling and we carefully checked for potential ant nests in the plant hollows. The ants foraging on foliage were removed by beating and manually. We expected potential individual ants to drop down after some time of separation from the colony. We placed tuna baits (one teaspoon under a gauze tied to the trunk of the tree) 20 cm above the Tanglefoot layer after the application of adhesive and checked for the presence of ants two hours later. All individuals were removed. Tanglefoot was reapplied every 3 – 4 weeks and new tuna bait was placed at the same place to confirm that ants were not present. Some ants crossed the

Tanglefoot barriers, so we excluded from the analyses all saplings with ant exclosures where ant activity exceeded 3 ants on any checking date (3 saplings in total).

To exclude all (ALL) predators (ants and vertebrate predators) we used a combination of the above-mentioned methods, i.e., by applying Tanglefoot to the trunk and by installation of the cage around the sapling, preventing the foliage from touching the cage and thus potential access of ants to the saplings. Supportive ropes used to hold the cages and lower part of the cage constructions were also covered by Tanglefoot to prevent new colonization by ants from neighbouring vegetation.

Measured variables

We sampled the effect of predator exclusion after 6 and 12 months (Table S2). This corresponded to the dry and wet season respectively (Table S2). Arthropod censuses were always performed destructively. First, all protective nettings were opened carefully where needed, and the trunk of the sapling was slowly lowered above a 2x2m mosquito net, wrapped into the net, and sprayed by fast knock-down insecticide (Mortein®). After a while, we shook the foliage firmly, opened the net, collected all arthropods (>1mm) and preserved them in vials filled with DNA grade ethanol. In the laboratory, arthropods were identified into orders or families, feeding specialization, life stage and measured to the nearest 0.1 mm (Table S3).

To assess herbivory leaf damage, we randomly selected two branches (ca. 50 leaves in total) and collected all leaves from them. We estimated how many other leaves in total were present on the sapling, and we used this number to calculate total leaf area of the sapling. Using a 50 x 50 cm^2 white background, we took photographs of flattened leaves collected from each sapling. Using Adobe Photoshop CS6 (Adobe Systems Inc., USA), we outlined the missing edges on the photographed leaves based on the expected shape. We then used ImageJ version 1.47 (National Institute of Health, USA) to calculate the remaining leaf area (a, in cm^2), the extrapolated leaf area without any herbivore damage (b), and the area lost to herbivory (c = b - a). We then estimated the percentage of leaf–area loss per m^2 of foliage and total standing leaf area per each whole focal sapling, using the count of the number of leaves (i.e., number of leaves * mean leaf area a) which we later used to calculate densities of arthropods per m^2.

We completed the second survey, on the same saplings, approximately six months after the first survey (Table S2). After the first survey, all exclosures were renewed and only some (N = 16) saplings (including their treatments) were replaced completely due to their death or damage (e.g., vandalism of villagers, fallen branches, landslides). The second survey was conducted exactly the same way as the first one, with the only difference being that *all* foliage was now collected from each sapling. We placed all leaves collected from individual saplings into a bag, randomly selected

ca. 50 leaves for photographing and further analyses, and weighted all leftover foliage as well as leaves used for photography. This allowed us to calculate total leaf area (from known weight and leaf area of leaves used to measure herbivorous damage) of the saplings more accurately than during the first survey. We found that herbivory in the leaves within a branch (i.e., herbivory on leaves from first survey; $P < 0.001$, $R = 0.854$) was corelated similarly to herbivory on leaves randomly collected within the whole plant (i.e., herbivory on leaves from first survey; $P < 0.001$, $R = 0.628$). Further, estimation of the leaf area for the plant (from first survey) was correlated ($P < 0.001$, $R = 0.358$) to the real leaf area calculated based on the leaf-weight (from first survey), despite some saplings grew significantly more than others during the season.

Bird survey

Bird communities have been repeatedly surveyed by point counts as a part of long-term monitoring, and we published the methodology and data in several separate studies (Marki, et al. 2016, Sam and Koane 2014, Sam, et al. 2019). Shortly, the point counts at each elevational site were carried out at 16 points regularly spaced along a 2,350 m transect (successive points were 150 ± 5 m apart to avoid overlap). All birds seen or heard within a fixed radial distance of 0 - 50 m were recorded. Each count lasted 15 min so that all 16 points were surveyed before 11:00 (i.e., such survey on all 16 points represents one replication in time). All points and all study sites were surveyed equally during two independent surveys.

In this study, we used data from two surveys conducted prior to and during the exclosure experiment. The first survey was conducted between 15th September and 15th October 2013 (3 first consecutive days from a larger study by Sam, et al. (2019). The second survey was conducted between 1st October 2015 and 2nd December 2015 (again 3 consecutive days per site). In the current analysis, we use abundances and species richness of 217 forest bird species recorded during the standardized point-counts, which represents 76.5% of the avifauna known from the region (Marki, et al. 2016). We include the earlier data from 2013 to calculate more robust mean abundances of insectivorous birds, as the 3 days long survey per site might not be sufficient for description of communities of tropical birds. Recorded birds (Table S4) were partitioned into five trophic guilds: insectivores, frugivores, frugivore-insectivores, insectivore-nectarivores and nectarivores, based on dietary information extracted from the literature (Hoyo, et al. 1992-2011, Pratt and Beehler 2015, Sam, et al. 2017). At the same time, body mass of each species was extracted and used to calculate total biomass of the birds at each elevation.

Bat survey

Bat communities were surveyed in the understory during two expeditions conducted in wet (February – March 2015) and dry seasons (June – July 2015). The method and data were published in Sivault, et al. (2022). Shortly, we used an ultrasonic bat call detector coupled with a recorder to detect echolocating bat species. We recorded bats at five points (i.e., 15 minutes per point), separated by 200 meters at each elevation, following the bird transect described above. Surveys were conducted for four days per site after sunset (6 pm) but were only feasible for two days at 3,200 and 3,700 m due to logistical problems. Recordings were analysed with Adobe Audition version 22.0. Echolocation call types were recognised from the recordings and then, identified based on information from other surveys (Sivault, et al. 2022). All bat species identified (Table S5) were perceived as strict insectivores based on the literature (Bonaccorso 1998, Flannery 1995). Despite a low sampling effort, we estimated bat activity as a proxy of relative abundance. We retained one bat pass per five-second interval, which is the mean duration of all bat species passes such as recommended by (Kerbiriou, et al. 2019). Finally, we calculated biomass of bats at each elevation using the average of the maximum body mass between males and females of each bat species found in the literature (Bonaccorso 1998, Flannery 1995). When information on body mass was missing, the body mass of the closest species was used (i.e., similar head-body size and/or forearm length).

Ant survey

The ant communities at each of the six study sites were sampled by hand collection. The trunk of each sapling was inspected for ants at breast-height for 10 minutes, and by a tuna bait method in May-June 2014. Commercial canned tuna in oil was used in baits, which is a standard method in the studies of foraging ant communities. One teaspoon of tuna was placed as a bait under a stripe of gauze at breast height at each of the saplings. Baits were inspected three hours following their exposure. Abundance of ants was counted on each bait and used in analyses. The combination of both methods was used to account for the fact, that not all ant species are attracted to baits (Véle, et al. 2009). Ant abundance data collected by tuna baits from understory saplings and hand collected from the trunks were used in correlations here. Despite the same survey being also conducted at 3200 and 3700 m above sea level, there were no ants recorded, which is in line with results from previous studies of ant communities conducted along the same gradient (Colwell, et al. 2016, Moses, et al. 2021, Sam, et al. 2015).

Data analysis

Arthropod densities: We used model selection and we determined the effect of our experimental treatments on arthropod densities using a linear mixed model. We used arthropod density (per m^2

of foliage) as our response variable and treatment, season and elevation and possible two-way interactions between them as our predictor variables. Elevation was modelled as a second-order polynomial to allow for non-linear elevation gradients. At each elevation, 3-7 tree species were selected for conducting our experiments, and across the 6 elevation bands between 200 m and 3700 m, a total of 18 tree species were used. Most tree species occurred in multiple elevation bands (see Table S1 for details). We used tree species as a random effect in our model to account for differences in baseline arthropod densities between species should be expected as they vary in their defensive traits. As each of the 560 focal saplings was surveyed twice, in wet and dry season, individual saplings were used as a second random factor.

Herbivory: Using model selection, we determined the effect of our experimental treatments on herbivory damage (as the proportion of the leaf area lost per m^2 of foliage) using a generalised linear mixed model with a beta error structure. As models with beta error structure only allow values between 0 and 1, the 0 values in our study (N = 2) were converted into 0.0001 prior to analysis. We used herbivory as the response variable, experimental treatment, elevation band and their interactions as predictor variables, and tree species as a random variable. Again, elevation was modelled as a second-order polynomial. We used the glmmTMB package (Brooks, et al. 2017) within R 4.0.2 (Team 2020) to build our generalised linear mixed models.

Body sizes: We modelled the mean body size of arthropods from each of the saplings, using a similar model to the described above for arthropod density.

Effect on groups of arthropods: We based this analysis on the unweighted natural log response ratios LRR (Curtis and Wang 1998, Hedges, et al. 1999) calculated from mean responses of individual groups of arthropods in the presence and absence of predators. LRR is an effect size measure that quantifies the results of experiments as the log-proportional change between the means of the treatment (in the absence of insectivorous predators, $\bar{x}_{I-}$) and control group (in the presence of insectivorous predators, $\bar{x}_{I+}$) and was thus calculated as ($\ln[\bar{x}_{I-}/\bar{x}_{I+}]$) for each of the three treatments at each elevational study site and season. After that, we conducted linear models, selected the best one and used function *get_model_data* from package *metan* to obtain the estimates of the effects (https://github.com/KatkaSam/GRAD_Exclosures).

Abundance, species richness and biomass of insectivorous birds and bats were correlated (Pearson correlation) with the log response ratio (LRR, calculated from the raw data) of the vertebrate exclosure treatment at each elevation. Number of saplings with ants on them and abundance of ants on baits were correlated with log response ratio LRR of the ant exclosure treatment at each elevation. All data were normalized on scale 0-1 and averages across both seasons

were taken, as the data from the predator surveys did not match exactly the timing of the experimental predator exclusion.

Results

Change in arthropod densities: In general, the density of arthropods was higher and increased more in the wet season than in the dry season (Table S6). Based on the model predictions, density of arthropods increased on average by 37% when the vertebrate predators were removed (Table S6). While the effect of vertebrates on arthropods was significant even when combined with the effect of ants (increase by 33%, Table S6), exclusion of ants alone had no significant effect on arthropod density, which increased only by 12% based on the model predictions (Table S6). The removal of the ants itself was successful, as there was total of 538 and 884 ants found on control saplings (CON) and on saplings protected against vertebrates (VER), but only 13 and 30 on saplings protected against both types of predators (ALL) and ants only were excluded (ANT) across the whole experiment. Thus, ants represented 2.3% and 1.9% of all arthropods in CON and VER saplings respectively but less than 0.05% of arthropods on ANT and ALL saplings. Elevation and the interaction between elevation and treatment and elevation and season had also significant effects on the resulting density of arthropods (Figure 1, Table 1).

Change in herbivory: Predator exclusion, elevation and season had a significant additive effect on leaf area loss (Figure 2, Table 1). The natural mean standing herbivorous damage on control saplings at 200 m a.s.l. was 2.24 ± 1.7% in the wet season and 2.49 ± 1.7% in the dry season and decreased with increasing elevation (see Sam et al. 2020 for more results). Overall, exclusion of insectivorous vertebrates as well as the exclusion of both types of predators (ALL) led to a significant increase in leaf damage by. 50 and 36% respectively (Table S7). However, the increase in leaf damage by ca. 9% in the ant exclosures was not significant (Table S7). Insects consumed significantly more leaf area in the wet than in the dry season (Figure 2). The increase of leaf damage seemed to be highest in the lowest and the upper most elevations (Figure 2, Table S7).

Change in mean body size of arthropods: Treatment, elevation, season, and interaction between elevation and treatment and elevation and season had an impact on the mean body sizes of arthropods (Figure 3, Table 1). Despite the season being selected as a significant factor based on model selection due to its importance in interaction, the season's effect by itself is not significant (Table 1). It means that seasonal effect cannot be described properly because it is different across elevations. The arthropods remaining in caged treatments were significantly bigger than arthropods collected from control saplings and saplings from which ants were excluded (Figure 3, Table 1). Despite the majority of the arthropods collected during the experiment being very small, arthropods

larger than ca. 2.2 cm were present only in the caged treatments (VER and ALL), to which vertebrate predators had no access (i.e., ANT, CON).

Changes in community composition: Overall, 12,177 arthropod individuals were identified as predatory arthropods, while only 4,085 were herbivores potentially responsible for chewing leaf damage and 10,065 were arthropods which had no relationship to chewing herbivory (Table S3). Majority of predatory arthropods (8,221) were spiders. Absolute abundance as well as relative abundances of spiders were higher in treatments where ants were excluded (both ALL and ANT) but the change was not detectable in vertebrate exclosures (VER) (Figure 4). Across the whole study, Araneae, Diptera, Hemiptera, and Lepidoptera larvae increased their abundances significantly after the removal of ants. Araneae, Coleoptera, Lepidoptera larvae, Orthoptera and all other arthropods increased their densities per m^2 of foliage on saplings from which the insectivorous predators were excluded. Densities of Hymenoptera (other than ants) and Hemiptera tended to decrease after the vertebrate predators were excluded (Figure 4).

***Predator communities and their relation to the observed effect*:** Overall, we found only weak relationships between the communities of predators and the cascades they cause. In general, the abundances of predators correlated with the effect measured on abundances of prey (Figure 5), but not on the effect measured on herbivory damage (Figure S2). This might be simply because the correlations between eight points do not allow robust analyses. Abundances of insectivorous birds, which could be potentially responsible for attacks, peaked at mid elevations (1700 - 2700 m) and correlated positively significantly (given the low power of the analysis and strong effect size) with the effect of vertebrate exclosure treatment on arthropod abundances ($R = 0.71$, $P = 0.049$, Figure 5a). Abundances of insectivorous bats decreased steeply from 200 to 1200 m a.s.l. and then peaked again at 2700m a.s.l. This pattern was again positively, but not significantly, correlated with the effect of vertebrate exclosure ($R = 0.56$, $P = 0.15$, Figure 5b). We detected more bats, and especially gleaning bats, in lowlands than at higher elevations (see also Sivault, et al. 2022 for more detailed results). It seems that our results indicate that bats are responsible at least partly for the predation at low elevations, while insectivorous birds are more important predators at the mid-elevations. Neither richness nor biomass of insectivorous birds or insectivorous bats correlated well with the effect of the exclosures measured on abundance of prey, and abundance of predators thus seemed to be a better correlate for predation pressure ($R < 0.21$, $P > 0.78$ in all cases). The number of trees on which ants occurred as well as ant's abundances decreased with elevations. Despite the positive relationship, neither number of trees with ants on them ($R = 0.25$, $P = 0.56$) nor abundance of the ants ($R = 0.14$, $P = 0.74$, Figure 5c) correlated with the effect of the ant exclosures on abundances of arthropods significantly.

Discussion

According to our first hypothesis (*H1*), predator removal increased arthropod richness on plants. Overall, arthropod richness increased by ca. 37% after the removal of insectivorous vertebrates, which is in line with the estimates from two global reviews reporting an increase by ca. 39% (Mooney, et al. 2010) and 69 % (Sam, et al., 2022). The effect of the removal of ants was overall rather low, with arthropod abundances increase by 12%, while the global effect of and removal is estimated to be ca. 12% (Sam, et al., 2022) but also up to more than 100% (Rosumek, et al. 2009). However, it is important to note that Rosumek's, et al. (2009) study analyses 70% datasets from myrmecophytic and only 30% non-myrmecophytic plants, while Sam's, et al. (2022) analyses mostly data from non-myrmecophytic plants. Similarly, the plant species used in the current study have no or very weak associations with ants. Moreover, it needs to be considered that the treatment itself led to nearly complete removal of the ants from our experimental saplings, and ants represented ca. 2% of all arthropods in samples from our controls, thus affecting the effect of the treatment on the total density of the arthropods.

The overall effect of predators on lower trophic levels was however affected by season (*H1A*). Predator exclosures had a smaller effect on arthropod richness in the dry season than in the wet season. The seasonal differences are likely to be much higher in more seasonal habitats than those of the northern side of nearly aseasonal Papua New Guinea where the experiment was conducted (Novotny and Basset 1998, Wright, et al. 1997). Also, birds seem to follow the patterns observed here (Bell 1982). Observations made during our long-term surveys indicate that most breeding of insectivores occurs the onset of rains, when the arthropods become more abundant as a response to leaf flushing (Sam, et al. 2015, Sam, et al. 2017), and which can together lead to strong effect of predator exclosures.

Contrary to our expectations (*H1B*) based on the productivity of the environment and earlier observed predation rate on dummy prey by birds along the same gradient (Sam, et al. 2015), the effect of insectivorous vertebrates on arthropod richness increased both towards the lowest (200 and 700m) and the higher elevations (above 2700m). We expected predator exclusion to have the highest effect between 700 and 1700 m a.s.l. where the abundances of insectivorous birds peaked. Our current results imply that the predation rate observed on dummy prey may not translate directly into the actual effect of predator exclusion, as there is an interplay between the natural abundances of arthropods and their predators. It is important to note again, that both groups of predators (birds and bats) were excluded in the current study. While the abundance of insectivorous bats was high at low and high elevations but low at mid-elevations, the abundance of insectivorous

birds peaked at the mid-elevations. Moreover, bat communities between lowlands and highlands are different, with most of the gleaners found in lowlands. Because the data has low power to detect subtle elevational trends, we can only speculate that bats are responsible, at least partly, for the predation at low elevations. In our study, predation risk on arthropods was correlated to the abundance of predatory birds (and less of the bats), supporting thus the hypothesis that predator density drives the effect of predation on lower trophic levels. These results are in line with some but not all earlier studies (Nordberg and Schwarzkopf 2019). Our data further indicates that the abundances of birds are a better correlate for the effect of predators than their richness or biomass. Especially because both species richness of birds decreases slowly and of bats steeply with increasing elevation, and this patter did not correlate with the abundances of respective taxa.

Predator exclusion affected not only arthropod densities but also their mean body sizes (*H2*). In general, the absence of insectivorous predators allowed larger arthropods to survive. This effect was detectable despite the mesh size (3x3 cm) of the cages excluding vertebrates was likely also preventing the access of large arthropods. Arthropod mean body size increased mainly at low elevations, where many large arthropods occurring (Sam, et al. 2017, Horne, et al. 2018), but also at the highest elevations. At the highest elevations, insectivorous birds were shown to be relatively large when compared to the available prey and feeding on the arthropods only partially. Despite suboptimally sized arthropod prey (ca. 6 mm) were found in their stomachs in a previous study (Sam, et al. 2017), the current results indicate that they also have capacity to suppress larger prey, which is in line with their body size (Sam, et al. 2017). In contrast to vertebrate insectivores, the exclusion of ants did not have any effect on the mean body size of arthropod communities. This is thus in contrast to results of an earlier study, where ants preyed selectively upon small-bodied caterpillars, increasing thus mean caterpillar length by 6% (Singer, et al. 2017). However, we believe that this is because ants hunt not only individually for tiny prey but also collectively for large arthropods, as shown in some ant species (Schmidt and Dejean 2018). This might lead to a balanced consumption of arthropods of all sizes.

Overall, the absence of predators allowed various groups of arthropods to increase their abundances (*H3*). First of all, insectivorous vertebrates did not affect ant density significantly, implying limited intraguild predation between these taxa in our study systems. The absolute numbers of ants increased on saplings protected against vertebrates, and ants represented very similar proportions of arthropods in samples from control and vertebrate-protected saplings. Also diet analyses of the birds from the same gradient did not find the ants to be important bird prey (Sam, et al. 2017). Based on literature, Coleoptera, Aranea, Lepidoptera larvae (Poulin, et al. 1994, Sam, et al. 2017) and many other smaller groups of arthropods (Bodawatta, et al. 2022, Poulin, et al.

1994), but no ants, were found to be preferred prey of birds (*H4*). This seems to be reflected in our current results, as these groups of arthropods increased their abundances significantly after the insectivores predators were removed, while other groups (e.g., Hymenoptera, Diptera, Hemiptera) did not respond strongly to the absence of predators. In the ant exclosures, Hemiptera, Lepidoptera, and Aranea increased their abundances significantly, but spiders seemed to be the most affected. This is in line with results of earlier studies according to which the spiders increased their abundances by more than 100% (Rosumek, et al. 2009) or by 84% (Sam, et al. 2022) in absence of ants. Even though our results can't resolve whether the spiders are typical prey of ants or their competitors, we believe that competition might be at least partially responsible for the patterns observed. Mainly because the increase of abundances of spiders was higher in absence of ants than in absence of vertebrates. Results of existing studies are vague, and despite most of the studies reporting ants to feed on eggs and insect larvae (Gathalkar and Sen 2018), there are both direct and indirect reports on ants hunting spiders (Risch and Carroll 1982).

In contrast to previous reports, the standing herbivory on control saplings along Mt Wilhelm was 5 to 10 times lower than the global estimates and we discuss this matter and potential reasons in an earlier study (Sam, et al. 2020). The change in the herbivory after the removal of predators was a further surprise (*H5*). Herbivory damage increased significantly both after removal of ants and vertebrate predators, yet the damage differed significantly in time and space. Across the whole gradient in the wet season, the herbivory increased by 112, 78 and 78% after the removal of all predators, vertebrate predators, and ants respectively. In the dry season, the increase was by 58, 52 and 42% respectively. All our results are thus higher than the earlier global estimates predicting increase of leaf herbivory by ca. 40 - 47% in absence of vertebrate predators (Mooney, et al. 2010, Sam, et al., 2022). Ant effect on herbivory was actually stronger that their effect on the density of herbivore arthropods only at low elevations, where ants increased herbivory by ca. 130% and herbivorous arthropods only by 3%. Similarly, Rosumek et al. (2009) detected that ant removal increased herbivory by more than 95% , whereas the abundances of herbivorous arthropods increased by ca. 60% in tropics.

Season had effect not only on the densities of arthropods, but also on the herbivory. The herbivory increased by ca. 100-230% in U shape pattern towards the lowest and higher elevations after the removal of vertebrate predators in wet season. During dry season, the biggest increase of herbivory after removal of vertebrates was detectable only above 2200m and ranged between the increase by 160% and by 555%. This pattern would suggest that insectivorous predators provide relatively better services to plants at the highest and lowest than at middle elevations. However, this is likely to be dependent on the plant defences and bottom-up control of the trophic cascades.

According to one hypothesis, plants are expected to invest progressively less into chemical defences with increasing elevation, because arthropod richness generally decreases towards higher elevations (Garibaldi, et al. 2011, Pellissier, et al. 2014). However, we did not observe very steep decrease in arthropod densities along our elevational gradient. Second hypothesis states that the costs of compensating for biomass lost to herbivory show a strong elevational increase too, due to nutritionally low and environmentally harsh higher elevations. Thus favouring higher investment into defences at the expense of growth by plants at higher elevations (Defossez, et al. 2018, Salgado, et al. 2016). Moreover, plants can defend their biomass directly and indirectly via help of insectivorous predators (Marquis and Whelan 1996). We can speculate that plants might not invest too much into direct defences at higher elevations as arthropods are relatively rare there, and insectivorous birds more abundant, but rely on indirect defences which work only in response to herbivory attacks instead. Even though this would generate a pattern in line with our observations, namely plants suffering high herbivory after the removal of insectivorous predators from the habitats at high elevations, this situation is unlikely, according to the existing knowledge about plant defences. In an earlier study from the same elevational gradient with several of the plant species studied here (Sam, et al. 2020), we concluded that elevational increase of defences (i.e., levels of alkaloids and flavonoids) was not a universal pattern, and several *Ficus* species from mid elevations were also well defenced (i.e., high protein precipitation capacity). Using analyses based on multiple traits of direct and indirect defences and linking them to datasets on arthropods herbivores would thus be necessary to understand elevational trends in plant defences.

In conclusion, we show that vertebrate insectivores suppress arthropods effectively, yet their impact differs among various groups of arthropods. The pressure of vertebrate insectivores is robust across the whole elevational gradient and translates to significant increase of plant herbivory in absence of predators. Our results imply that relative contribution of birds and bats differs along the elevational gradient. In contrast, ants do not suppress arthropods significantly, yet the trophic cascades caused by them do translate into increased herbivory at the most productive sites of the elevational gradient, where the abundances of ants are also the highest. Insectivorous vertebrates, but not ants, had a stronger negative effect on large arthropods which can further negatively impact herbivory rates. While generalities emerge, we suggest that intraguild predation and mesopredators, plant defences and also more detailed predator surveys need to be considered in future experiments, as they significantly affect the strength of trophic cascades.

Figure 1. Effect of the predator exclusion (treatment) on the densities of all arthropods from saplings along the elevational gradient of Mt Wilhelm in wet (a) and dry season (b). Each individual data point shows the resulting density of arthropods (per m^2 of foliage) on a focal sapling. Curves show predicted values from the linear model, including season, elevation and treatment and interaction between elevation and treatment as a fixed factor and plant species and identity of the sapling as a random effect. Treatments: CON = control saplings with free access of predators, ANT = saplings from which ants are excluded by tangle glue, VER = = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded.

Figure 2. Effect of the predator exclusion(treatment) on leaf damage (m^2 per sapling) on saplings along the elevational gradient of Mt Wilhelm in wet (a) and dry season (b). Each individual data point shows the resulting herbivory damage of a focal sapling. Curves show predicted values from the glmmTMB models , including season, elevation and treatment as fixed factors and plant species and identity of the sapling as a random effect. Treatments: CON = control saplings with free access of predators, ANT = saplings from which ants are excluded by tangle glue, VER = = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded.

Figure 3. Effect of the predator exclusion on mean body size of the arthropods collected from saplings along the elevational gradient of Mt Wilhelm in wet (a) and dry season (b). Each individual data point shows the resulting mean body size of the arthropod community of the given sapling. Curves show predicted values from the linear model, including season, elevation, and treatment as a fixed factor . See Table S6 for the results of the considered models. Occurrence (log of the total abundance) of the arthropods of given body size in the four treatments (c). Treatments: CON = control saplings with free access of predators, ANT = saplings from which ants are excluded by tangle glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded.

Figure 4. Mean proportion of the spiders in an average sample from control treatments (grey area) and in insectivorous vertebrate (VER - magenta line), and ant exclosure (ANT - blue line) and in exclosure where both insectivorous vertebrates and ants were excluded (ALL- yellow line) across the elevational gradient (a). Caterpillar graph showing the difference how individual orders of arthropods responded to the predator exclosure treatments. X-axis shows mean effect sizes of

natural log ratios (LRR = ln(exclosure/control)) with 95% CI of individual response variables. Effect size values above zero indicated that the absence of predators (treatment) was more harmful to plants than control (presence of predators), as the abundances of arthropods in exclosures increased and caused potentially higher herbivory damage to plants (b). Treatments: ANT = saplings from which ants are excluded by tangle glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded.

Figure 5. Correlations between effect of vertebrate (a, b) and ant (c) exclosure (LRR calculated from raw data, normalized data) on abundances of arthropods and abundances (normalized) of insectivorous birds (a), insectivorous bats (b) and ants (c) potentially feeding on the experimental saplings.

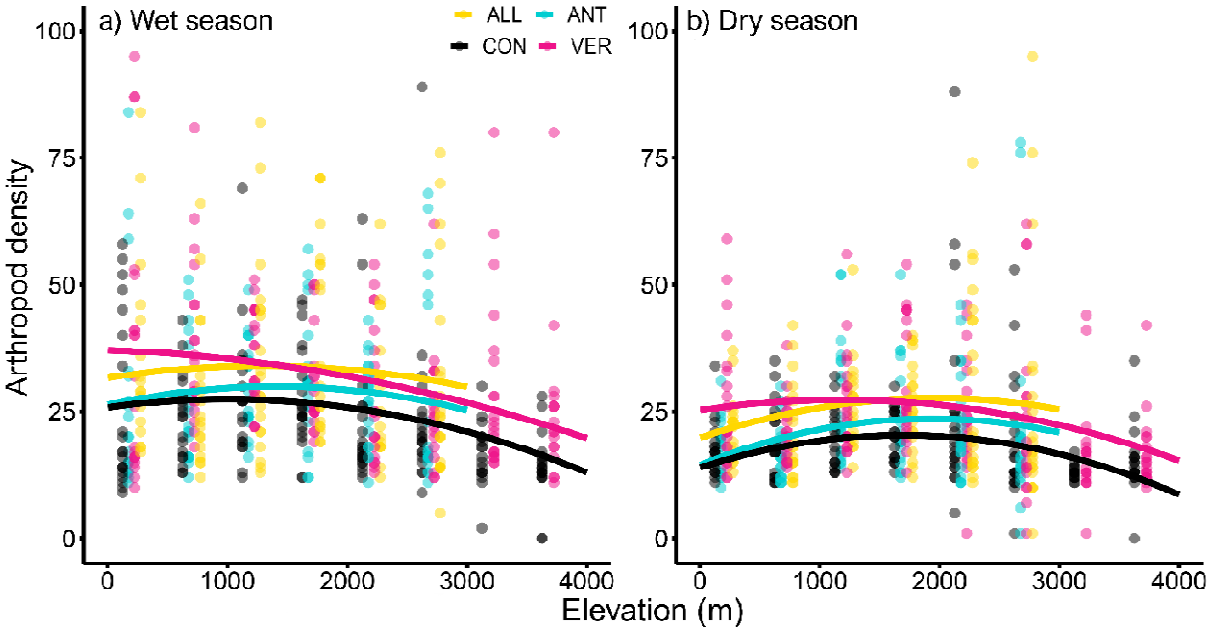
a) Wet season
b) Dry season
ALL
ANT
CON
VER
Arthropod density
Elevation (m)
0
25
50
75
100
0
1000
2000
3000
4000

Figure 1.

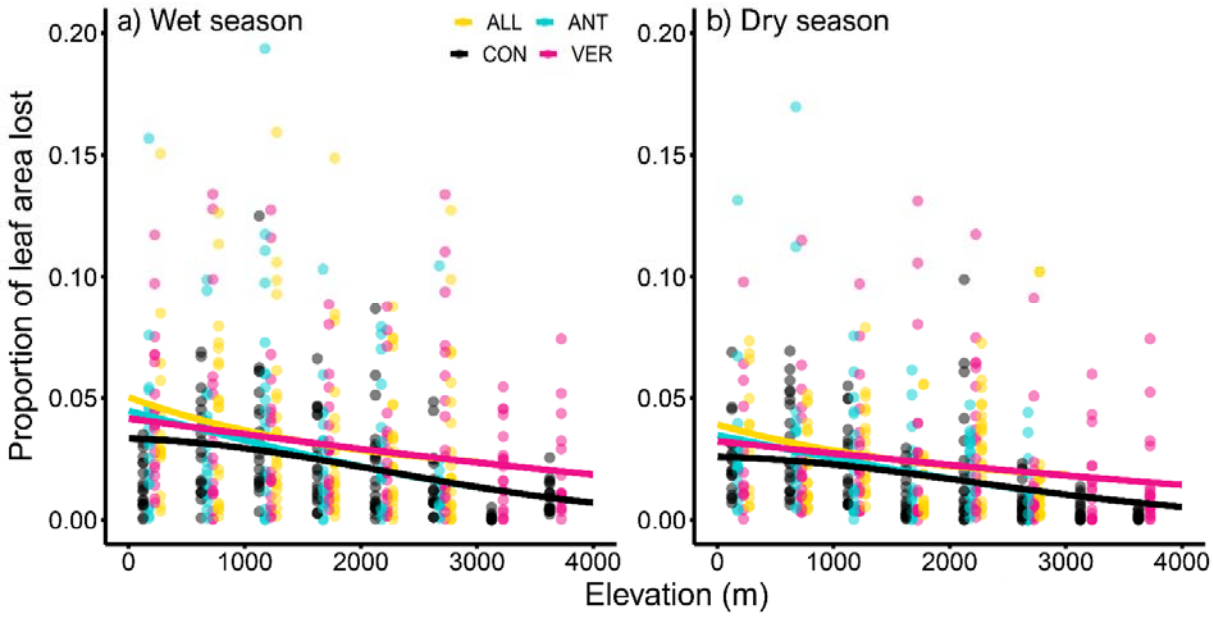
a) Wet season
b) Dry season
ALL
ANT
CON
VER
Proportion of leaf area lost
0.20
0.15
0.10
0.05
0.00
0
1000
2000
3000
4000
Elevation (m)

Figure 2.

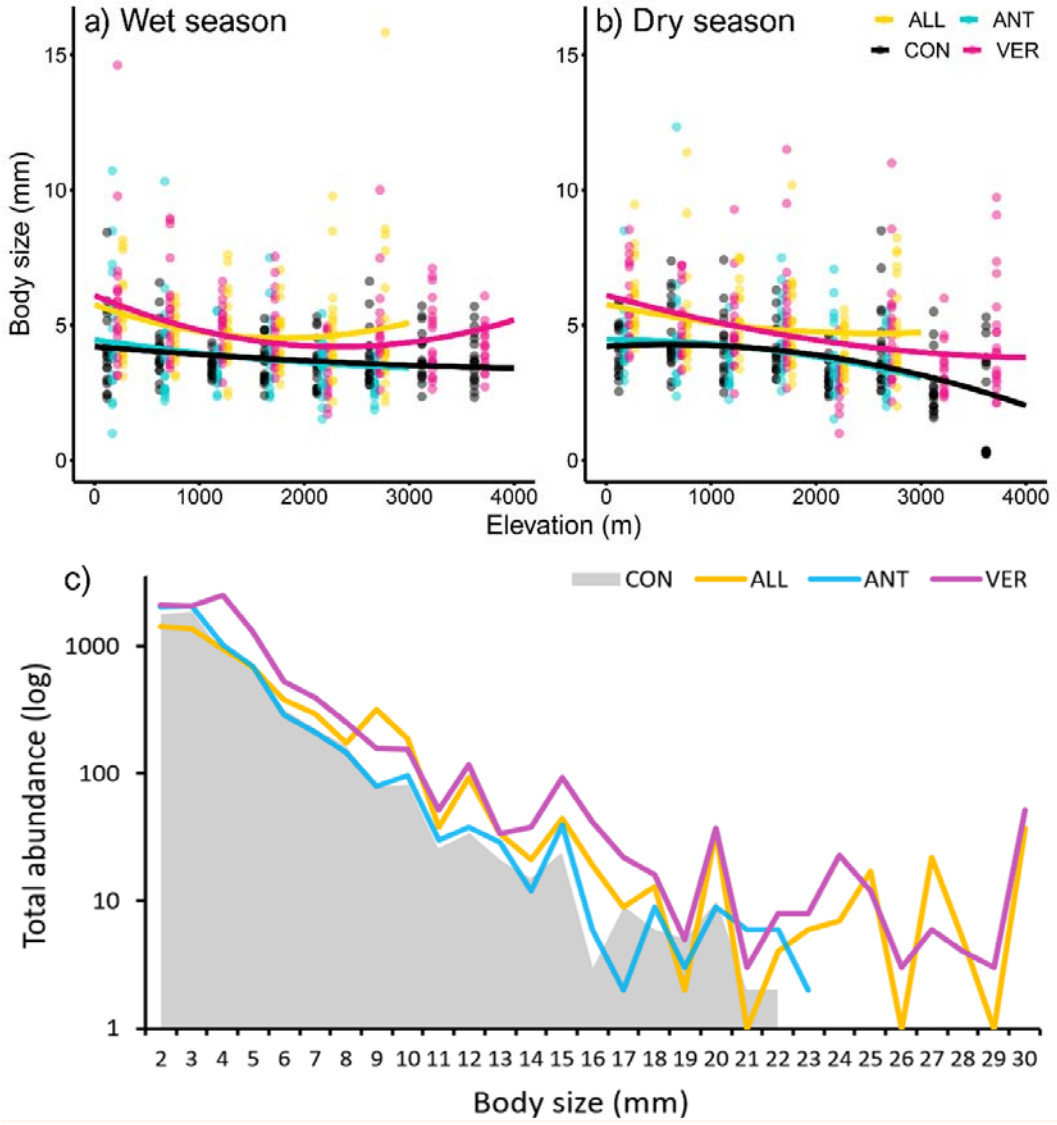
a) Wet season
b) Dry season
ALL
ANT
CON
VER
Body size (mm)
Elevation (m)
c)
Total abundance (log)
Body size (mm)

Figure 3.

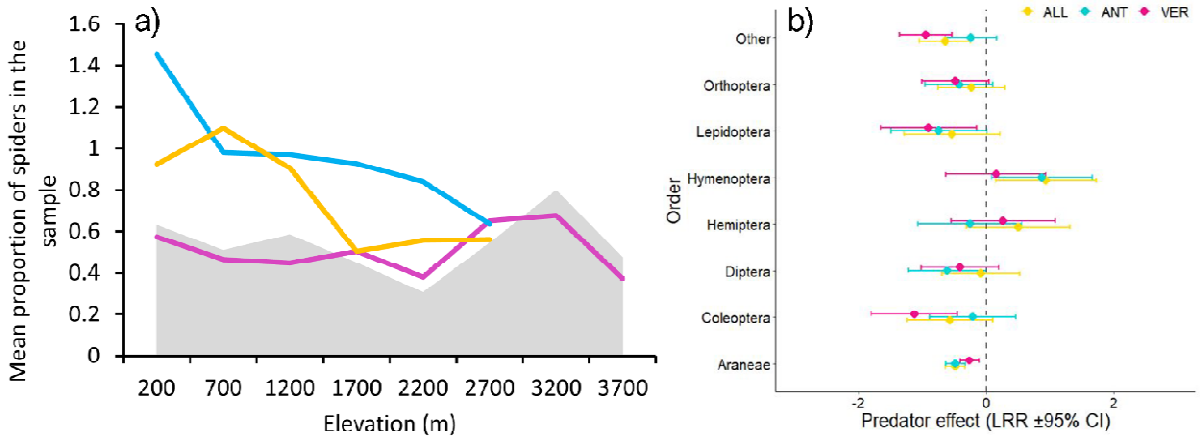
a)
Mean proportion of spiders in the sample
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
200
700
1200
1700
2200
2700
3200
3700
Elevation (m)
b)
ALL
ANT
VER
Order
Other
Orthoptera
Lepidoptera
Hymenoptera
Hemiptera
Diptera
Coleoptera
Araneae
-2
0
2
Predator effect (LRR ±95% CI)

Figure 4.

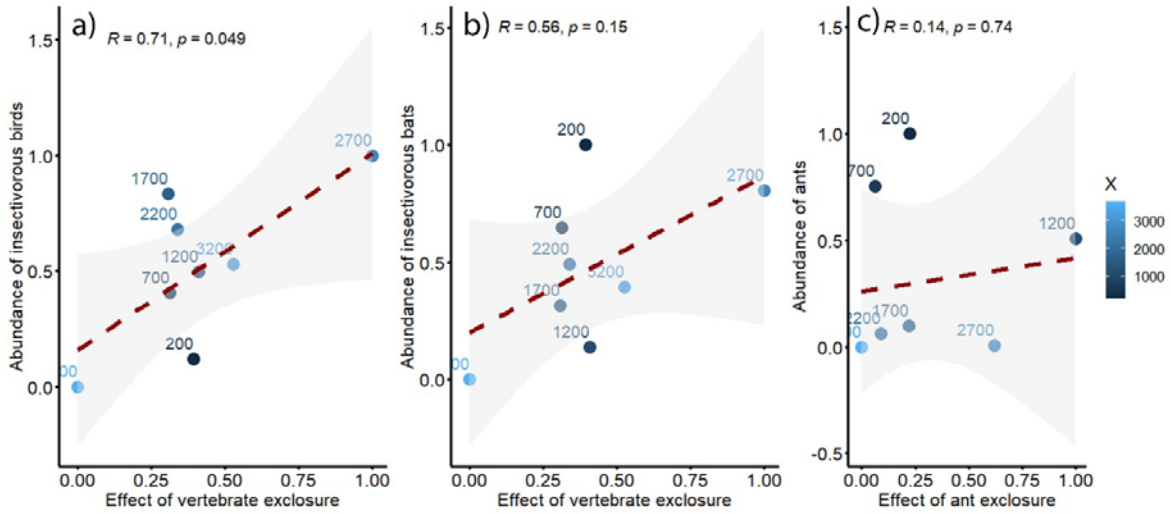
a)
R = 0.71, p = 0.049
Abundance of insectivorous birds
Effect of vertebrate exclosure
b)
R = 0.56, p = 0.15
Abundance of insectivorous bats
Effect of vertebrate exclosure
c)
R = 0.14, p = 0.74
Abundance of ants
Effect of ant exclosure
X
3000
2000
1000

Figure 5.

Table 1. Corrected Akaike Information Criterion (AICc) for regression models for abundances for all arthropods, herbivory damage, and mean body size of arthropods observed on saplings protected from the access of various predators (treatment) in wet and dry season (season) along the elevational gradient of Mt. Wilhelm (elevation) in Papua New Guinea (a). Results of the analysis of variance of the most parsimonious models selected based on the AIC (b).

	Arthropod abundances		Herbivory		Body sizes	
	dAICc	df	dAICc	df	dAICc	df
Null	216.1	4	102.5	4	162.2	4
Treatment	174.5	7	80.3	7	86	7
Elevation	186.2	6	50.2	6	129.8	6
Season	140	5	75.6	5	167.1	5
Treatment + Season	97.9	8	52.3	8	90.9	8
Treatment + Elevation	145.3	9	25.8	9	48.1	9
Season + Elevation	110.6	7	25.7	7	90.9	8
Treatment : Season	87	11	60.2	11	93.9	11
Treatment : Elevation	133	12	47.7	12	89.6	12
Season : Elevation	165.6	8	52.1	8	106.7	8
Treatment : Season + Elevation	58.5	13	7.4	13	56	13
Treatment : Elevation + Season	57.4	13	22.9	13	94.6	13
Season : Elevation + Treatment	124.7	11	27.9	11	24.9	11
Treatment + Elevation + Season	69.2	10	0.3	10	53	10
Treatment + Elevation + Season + Treatment : Elevation	21.5	16	0	16	23.3	16
Treatment + Elevation + Season + Treatment : Season	61.3	13	5.4	13	56	13
Treatment + Elevation + Season + Elevation : Season	47.7	12	0.8	12	29.8	12
Treatment + Elevation + Season + Elevation : Season + Elevation : Treatment	0	18	0.5	18	0	18
Treatment + Elevation + Season + Elevation : Treatment + Season : Treatment	13.6	19	4.8	19	26.3	19
Treatment + Elevation + Season + Elevation : Treatment + Season : Treatment + Season : Elevation	7.8	21	5.3	21	8	21
Results of the best model	Chisq (df)	P	Chisq (df)	P	Chisq (df)	P
Elevation	24.41 (2)	<0.001	73.18 (2)	<0.001	50.13 (2)	<0.001
Treatment	43.58 (3)	<0.001	30.87 (3)	<0.001	104.21 (3)	<0.001
Season	83.22 (1)	<0.001	28.21 (1)	<0.001	0.23 (1)	0.632
Elevation : Treatment	5.09 (6)	0.532	12.57 (6)	0.051	11.87 (6)	0.065
Elevation : Season	9.78 (2)	0.011			19.95 (2)	<0.001

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