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Faculty of Science

Roles of bats in top-down forces across elevations, strata, and latitudes

Ph.D. Thesis

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Annotation

In this thesis, I delve into the top-down regulation of arthropods and its indirect effects on herbivory, with a focus on the crucial role of bats as insect predators across different spatial scales. My primary objective was to enhance our understanding of bat ecology and their contribution to top-down control, comparing it to other predators across elevations of a tropical mountain. I found that only birds and bats have a significant impact on top-down control of herbivory across seasons and elevations. Additionally, this inquiry extended to evaluating the contributions of both birds and bats to top-down control in both the forest understory and the forest canopy of a temperate forest. I found that they both play a consistent role in preserving ecological balance across different layers of the forest. Finally, I explored this aspect in diverse temperate and tropical understory forests located at different latitudes. I found that birds and bats have consistent and comparable effects on arthropod densities across latitudes. However, I observed that top-down control of herbivory increased in forests rich in bat and bird species. Overall, this research underscores the critical importance of recognising bats as key predators influencing top-down forces within forest ecosystems. Furthermore, my findings highlight the complexity and interconnectivity of relationships across different trophic levels in undisturbed forests. This thesis paves the way for further research in other mountainous regions and diverse geographical areas.

Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

Elise Sivault

České Budějovice,

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This thesis originated from a partnership of **Faculty of Science**, **University of South Bohemia**, and **Institute of Entomology, Biology Centre of the ASCR**, supporting doctoral studies in the **Zoology** study programme.

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I would like to express my gratitude to all my colleagues who have made my time at work, and more broadly, my life in the Czech Republic enjoyable. I particularly cherish the memories of our international dinners, movies, board games, dancing, and karaoke nights, among others. While the list of names is extensive, I want to specifically mention my flatmates, Sara and Xue, as well as colleagues and friends Pedro, Shafia, Marketa, Yvonne, Fred, Ernesto, Tanisha, Mar

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Completing this thesis has been a challenging yet rewarding journey, and I am thankful for the collective efforts that have made it possible.

List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

Chapter 1:

Sivault, E., Amick, P. K., Armstrong, K. N., Novotny, V., & Sam, K. (2023). Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. Biotropica, 55(1), 81-94. https://doi.org/ 10.1111/btp.13161 (IF = 2.1).

PKA conducted the fieldwork, recorded bat calls, and mist-netted the bats. KNA and ES performed bat call identifications. ES performed data analyses, extracted data from literature, and wrote the first draft of the manuscript. KS designed and funded the study and helped with the analyses. PKA, KNA, KS, and VN contributed significantly to revisions.

Chapter 2:

Sam, K., Jorge, L. R., Koane, B., Amick, P. K., & **Sivault, E.** (2023). Vertebrates, but not ants, protect rainforest from herbivorous insects across elevations in Papua New Guinea. Journal of Biogeography, 50(10), 1803-1816. https://doi.org/10.1111/jbi.14686 (IF = 3.9).

KS conceived the ideas, secured funding, and conducted the experiment with help of BK. PKA and ES conducted the survey of insectivorous predators, LRJ assisted with statistical analyses to ES and KS. All authors contributed to writing and edited the first draft written by KS and ES.

Chapter 3:

Sivault, E., Koane, B., Chmurova, L., & Sam, K. Birds and bats reduce herbivory damage in Papua New Guinean highland forests. Manuscript.

BK, LC, and KS conducted the fieldwork, ES performed data analyses and wrote the first draft of the manuscript, KS designed and funded the study and helped with the analyses, and BK, LC and KS contributed significantly to revisions.

Chapter 4:

Sivault, E., Kollross, J., Re Jorge, L., Finnie, S., Diez-Méndez, D., Fernandez Garzon, S., Maraia, H., Lenc, J., Libra, M., Murakami, M., Nakaji, T., Nakamura, M., Sreekar, R., Sam, L., Abe, T., Weiss, M., & Sam, K. Insectivorous birds and bats outperform ants in the top-down regulation of arthropods across strata of a Japanese temperate forest. Manuscript.

ES and JK should be considered joint first author. ES, JK, SF, SFG, HM, JL, ML, MM, TN, MN, RS, LS, TA, and KS conducted the fieldwork and collected the data; MW and JK led the arthropod sorting and identification; KS and HM led the leaf herbivory analysis with the support of several undergraduate students; ES, SFG and RS led the bat, ant and bird surveys, respectively; ES and LRJ performed the data analyses; KS designed and funded the study and helped with the analyses; ES and JK wrote the first draft of the manuscript. All authors contributed significantly to revisions and gave final approval for publication.

Chapter 5:

Sivault, E., Fernandez Garzon, S., Finnie, S., Houska Tahadlova, M., Jančúchová Lásková, J., Re Jorge, L., Kollross, J., Lenc, J., Libra, M., Maraia, H., Philip, A. J., Vlasatá, T., Weiss, M., Xiao, X., & Sam, K. Top-down control of herbivory intensifies towards the most bird and bat species-rich forests. Manuscript.

ES, JK, MHT, AJP, XX, SF, SFG, HM, JL, ML, MW and KS conducted the fieldwork and collected the data, MW led the arthropod sorting and identification, KS, HM, TV, and JJL led the leaf herbivory analysis with the support of several undergraduate students, ES performed the data analyses, LRJ helped with the analyses, KS designed and funded the study, ES wrote the first draft of the manuscript and all co-authors contributed significantly to revisions.

Co-author agreement

Katerina Sam, the supervisor of this thesis and first author of Chapter 2 and co-author of Chapters 1 to 5, fully acknowledges the contribution of Elise Sivault as the first and co-author and her contributions as stated above.

Mgr. Katerina Sam, Ph.D.

Table of Contents

1.Introduction

1.1. Bats: key predators in forest ecosystems

Bats (order: Chiroptera) make up about 22% of all mammal species, with a total of over 1,462 known species worldwide (Simmons & Cirranello, 2023). Their morphological variability is considerable, ranging from species with a wingspan of 1.7 m to species reaching a body weight of 2 grams. This variability has profound implications for their feeding and foraging behaviour. Indeed, bats exhibit an impressive ecological diversity, spanning all trophic levels (nectarivory, frugivory, sanguivory, piscivory, carnivory and insectivory) and hunting strategies (fishing, trawling, active and passive hunting). They inhabit a wide range of environments, including wetlands, forests, grasslands, farmlands, and urban areas that include both open and densely cluttered areas.

Nevertheless, almost 70 % of the species known are insectivorous (Fenton & Simmons, 2015). They have a high ability to consume insects, with some estimates suggesting a daily consumption of up to 100 % of their body weight when active (Coutts et al., 1973; Kalka & Kalko, 2006; Kurta et al., 1989), highlighting their potential in suppressing arthropod populations. Most insectivorous bats are considered generalist predators, more specifically opportunistic foragers, meaning that they can adapt their predatory activity depending on prey abundance (Blažek et al., 2021; Charbonnier et al., 2014; Clare et al., 2014; Heim et al., 2017). Hence, the various foraging strategies and morphologies of bat species, together with spatial and temporal changes in prey communities, may lead to considerable variation in the strength of the predation pressure by bats.

Although bats are found all over the world, they predominantly inhabit forested areas (Maas et al., 2016). Forests provide an abundance of diverse food sources and serve as important roosting and breeding sites, offering protection from predators and adverse weather conditions (Dietz et al., 2018; RuczyńSki & Bogdanowicz, 2005). Like many other taxonomic groups, bat populations are influenced by both continental and local processes. Factors such as latitude (Bogoni et al., 2021; Raz et al., 2023) and elevation (McCain, 2007, 2009) play an important role in shaping their regional biodiversity. In addition, the overall quality of the habitat, as studied by Charbonnier et al. (2016), further contributes to the composition of the regional species pool.

Due to their important ability as flying mammals to colonise, bats are also found on many islands. As predicted by the theory of island biogeography and the species-area relationship (MacArthur & Wilson, 2001; Whittaker & Fernandez-Palacios, 2007), larger islands, which have greater topographic and habitat heterogeneity, tend to harbour a greater number of bat species (Carvajal & Adler, 2005; Frick et al., 2008). Yet, compared to other vertebrates, studies that aim to understand the patterns of bat species diversity are scarce (Bogoni et al., 2021; McCain, 2007), with some geographical regions largely underrepresented, including hyper-diverse large islands like Papua New Guinea (**Chapter 1**).

1.2. Quantifying the role of bats in top-down forces

Trophic interactions involve the transfer of energy between different trophic levels within a food chain or food web. However, a food web goes beyond a simple linear food chain that represents a single energy pathway. Instead, it constitutes a complex and interconnected network of food relationships involving different species and trophic levels within an ecosystem and encompassing multiple food chains. In this thesis, I focus on the tri-trophic interactions between plants, arthropods (especially, chewing herbivores) and predators among the myriad possible trophic interactions.

Predators that prey on herbivorous arthropods can benefit plants by either preventing or hindering the feeding activities of these herbivorous arthropods (Hermann & Thaler, 2014; Kozlov et al., 2017). They thus establish what is commonly referred to as top-down control or trophic cascade, in which the actions of one trophic level in the food chain can influence the abundance or behaviour of species at other trophic levels. This contrasts with bottom-up control, in which plants control herbivores through plant defences that either limit resources for herbivores or force them to cope with a variety of defences.

Through top-down control, bats as predators of arthropods have demonstrated the ability to reduce the density of arthropod herbivores (Cassano et al., 2016; Maas et al., 2013; Ocampo-Ariza et al., 2023; Figure 1, II), which consequently leads to reduced damage to plants (Kalka et al., 2008; Morrison & Lindell, 2012; Figure 1, III). However, due to the complexity of trophic interactions, in some cases bats have also been observed to consume predatory arthropods (Gras et al., 2016; Karp & Daily, 2014; Maas et al., 2013; Ocampo-Ariza et al., 2023), which in turn feed on herbivores (Figure 1, IV). Therefore, this may partially or fully offset the negative effect of bats on herbivore arthropods and consequently their positive effect on plants (Figure 1, III). Nevertheless, bats are often overlooked compared to other insectivorous predators (e.g., birds) (Greenberg et al., 2000; Philpott et al., 2004; Van Bael et al., 2003), and questions remain about their relative contribution to top-down control (**Chapters 3, 4, 5**).

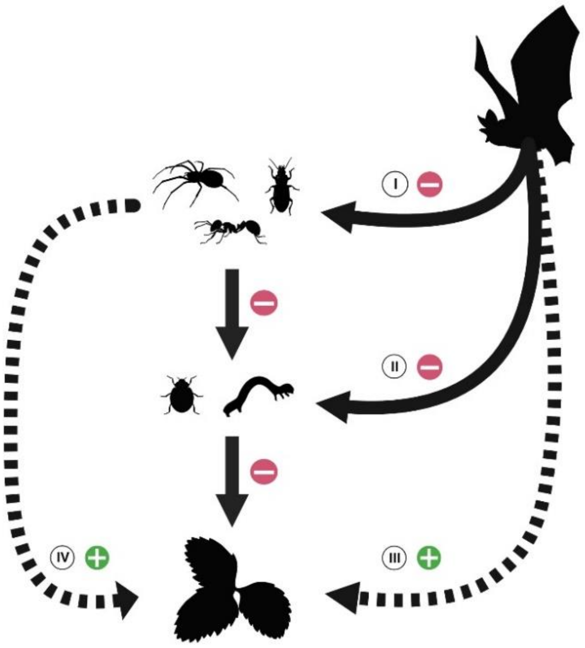

Figure 1: Diagram of trophic cascades initiated by bats, acting as apex predators of arthropods in an ecosystem. Bats primarily prey on herbivores (II), thus reducing plant damage (III). Additionally, bats occasionally target predatory arthropods (I), and these predatory arthropods, in turn, contribute to the reduction of plant damage (IV). It is noteworthy that a higher consumption of predatory arthropods (I) compared to herbivores (II) can potentially reverse the positive and indirect impact of bats on plants (III), transforming it into a detrimental effect. Dashed arrows represent an indirect effect.

Nevertheless, bats are not the only predators of arthropods. For instance, birds, predatory arthropods (e.g., ants), as well as pathogens and parasitoids have been thoroughly studied as insect enemies (Hawkins et al., 1997; Memmott et al., 2000; Van Veen et al., 2008). The combined predatory activity of multiple groups may have three main effects: (a) additive effects, where each predator group contributes independently to the overall reduction in arthropod populations (Morrison & Lindell, 2012; Williams-Guillén et al., 2008); (b) synergistic effects that may occur when the interaction between predator groups enhances their overall effectiveness in controlling arthropod populations (Losey & Denno, 1998); and (c) antagonistic effects that may manifest if the presence of one predator group interferes with the effectiveness of another, resulting in a reduced overall impact on arthropod control (Ferguson & Stiling, 1996; Martin et al., 2013; Mooney, 2007). Understanding these dynamics is crucial for a complete picture of how different groups collectively regulate arthropod populations in an ecosystem.

The assessment of top-down control exerted by predators, such as birds and bats, on herbivorous insects is most effectively accomplished by predator exclusion experiments (Maas et al., 2019). These experiments simulate the absence of flying vertebrates, allowing for the direct measurement of the effects by observing herbivore damage or shifts in the arthropod community (e.g., Kalka et al., 2008; Karp & Daily, 2014; Morrison & Lindell, 2012).

Additionally, they enable the distinction between group-specific and combined impacts of predators on arthropod communities (e.g., Maas et al., 2013; Ocampo-Ariza et al., 2023; Williams-Guillén et al., 2008). Indeed, mesh nets are used to enclose focal plants preventing birds and bats from foraging but allowing access to arthropods. To measure the relative impact of birds and bats on arthropods, group-specific exclosures can be activated at different times of the day, selectively excluding diurnal birds or nocturnal bats whereas the combined contribution of birds and bats can be assessed by permanent exclusions.

Unravelling the complexity of trophic cascades involving multiple predator types within the same community, and their cascading impacts on plants, remains a significant and unresolved challenge in ecology. The outcomes are likely to be context-dependent, influenced by factors such as habitat characteristics, landscape context, and intricate multitrophic interactions (e.g., Gras et al., 2016; Martin et al., 2013; Martínez-Salinas et al., 2016). While these relationships are increasingly well understood at certain local scales, contrasting (Karp et al., 2018) or missing patterns emerge at larger spatial scales, such as across elevations (**Chapters 2, 3**), strata (**Chapter 4**), or latitudes (**Chapter 5**).

1.3. Top-down control across elevations

Elevational gradients provide accessible and controlled natural experiments that allow researchers to investigate the influence of abiotic factors and spatial variation in ecological processes such as trophic cascades. Specifically, they avoid confounding effects associated with latitudinal gradients, such as dispersal limitation (Salisbury et al., 2012), allow comparisons of intra- and inter-specific patterns at the same scale and within the same climatic ranges (e.g., Beck et al., 2017; Colwell et al., 2016), and are replicable within and between regions (e.g., Grytnes et al., 2014; Sanders, 2002).

Increasing elevation induces variations in abiotic factors such as a reduction in nutrient availability (Fisher et al., 2013; Salinas et al., 2011; Ramesh et al., 2023), a linear decrease in temperature (Barry, 2008) and generally, increases in precipitation (McCain & Grytnes, 2010) and solar radiation (Barry, 2008). These changes, in turn, have indirect effects on the broader biotic context that shapes the identity, abundance and interactions of predator, plant, and herbivore communities (McCain & Grytnes, 2010), likely altering the strength of top-down forces across elevations (Roslin et al., 2017; Sam et al., 2015).

For example, in the case of bats, studies have demonstrated that species richness tends to decrease with elevation in most tropical regions or follows an unimodal trend in temperate regions (McCain, 2007; McCain & Grytnes, 2010). It has been suggested that the peak in bat species richness occurs in elevational zones where both water availability and temperature are high simultaneously. This typically corresponds to low and mid-elevations in tropical mountains and temperate mountains, respectively (McCain, 2007). These variations in species richness and likely in functional diversity may result in significant changes in the contribution of insectivorous bats to top-down forces with increasing elevation.

Yet, many predator exclusion experiments have been conducted at a single location (Beilke & O’Keefe, n.d.; Kalka et al., 2008; Philpott et al., 2004; Williams-Guillén et al., 2008), sometimes for only a single season (Cassano et al., 2016; Ferreira et al., 2023; Gras et al., 2016; Kalka et al., 2008; Maas et al., 2013), making it difficult to determine how trophic interactions are affected by variations in climate and other environmental factors. Thus, research is needed to investigate the consequences of elevational changes on top-down interactions mediated by predators by comparing effects across multiple elevations (**Chapters 2, 3**).

1.4. Top-down control across forest strata

Given the complexity of food webs, the extent of top-down control varies depending on the context, resulting in fluctuations not only among different forests but also within different vertical strata of a single forest (Böhm et al., 2011; Van Bael et al., 2003). Forests are composed of multiple layers or strata, each characterised by specific types of vegetation, light availability, and ecological niches. In this thesis, I focus solely on the canopy and understory layers of the forest as they represent two distinct extremes along the vertical gradient.

The canopy, situated higher up, is more exposed than the understory to thermal and hydric changes (De Frenne et al., 2021). In general, it experiences warmer temperatures, higher sunlight and wind exposure and lower humidity levels than the understory (Parker, 1995). Differences in tree height, tree disposition, free space, plant biomass, and the size and abundance of leaves, flowers, and seeds, are examples of other crucial factors distinguishing the canopy from the understory (Lawton, 1983). These differences contribute to the development of unique ecological niches that have significant implications for the quantity and quality of food resources available to arthropods (Basset, 2001), ultimately shaping their distribution as well as that of their predators who are expected to follow them.

There is a growing body of documentation on the vertical stratification of arthropods and their predators in forests (Basham et al., 2023; de Souza Amorim et al., 2022; McCaig et al., 2020). A recent review (Basham et al., 2023) suggested that in the tropics, bat stratification was variable among study sites but globally trended towards greater richness and abundance in the canopy. In contrast, inconsistent patterns emerge in temperate forests, with no layer preferences within guilds (Froidevaux et al., 2014) or species-dependent activity differences between strata (Erasmy et al., 2021; Plank et al., 2012). The differences can largely be explained by the foraging behaviour (Bernard, 2001), roost site selection (Wunder and Carey, 1996), predator avoidance (Rex et al., 2011) of bats, along with competition for space and resources, as frequently observed in other vertebrates (Chmel et al., 2016; Rader & Krockenberger, 2006).

However, limited access to the canopy has often impeded investigations into more complex ecological questions. Uncertainties persist regarding the role of stratification in trophic cascades and comparisons of top-down forces within habitats remain relatively unexplored (Böhm et al., 2011; Van Bael et al., 2003; **Chapter 4**).

1.5. Top-down control across latitude

Like elevational gradients, latitudinal gradients serve as natural laboratories for studying ecological processes. However, the factors that change between latitudes are more diverse and complex and are influenced by historical, geographical, biotic, abiotic, physical and stochastic variables (Mittelbach et al., 2007; Mittelbach & Schemske, 2015). Indeed, latitudes differ due to the interplay of primary environmental gradients (temperature, solar radiation, seasonality, etc.) that are correlated with each other, making direct tests of hypotheses difficult and often controversial. This complexity poses a major challenge for science to provide a comprehensive explanation.

Nevertheless, previous research has emphasised the increasing influence of top-down forces on herbivores in tropical regions (Rodríguez-Castañeda, 2013; Roslin et al., 2017; Zvereva et al., 2020), which is consistent with the ecological concept that biotic interactions are more pronounced at lower latitudes (Pennings & Silliman, 2005; Schemske et al., 2009). The expectations of greater diversity and density of predators such as birds and bats in tropical forests compared to temperate forests (Maas et al., 2016) support this concept. However, the debate over the strength of top-down forces along latitudinal gradients remains open, with some studies suggesting that there is no variation in productivity levels (Borer et al., 2006; Mooney et al., 2010). Furthermore, due to the complexity of food webs and the influence of local conditions, it is likely that top-down forces vary from site to site (Gripenberg & Roslin, 2007).

Certainly, similar to the shifts in elevation, changes in latitude and the various abiotic and biotic factors associated with it are likely to lead to variations in the strength of bat-mediated trophic cascades. This influence relies on the richness, density, and functional diversity of the insectivorous bat assemblage in the specific region. Nevertheless, there is limited available evidence regarding the significance of bats in multitrophic food webs and their role in suppressing arthropods across diverse geographic regions (**Chapter 5**).

1.6. Thesis Overview

In this thesis, I investigated the top-down regulation of arthropods and the indirect effect of predation on plants across different spatial scales, unravelling the importance of bats as predators of insects (Figure 2).

In **Chapter 1**, I examined the species richness and assemblages of bats along an elevational transect in Papua New Guinea, where studies are scarce, and species understudied. Bats were captured and recorded at eight elevations, and comparisons at the assemblage level were conducted using various biotic and abiotic factors to uncover the drivers of these variations. This chapter served as a basis for the following research.

In **Chapter 2**, to depict which predators are causing a major top-down control of arthropod communities and herbivory damage with changing elevation in tropical forest understories, I conducted predator exclusion experiments. Specifically, I excluded flying vertebrates (i.e., birds and bats together) and ants along the same elevational transect employed in Chapter 1, subsequently collecting arthropods, and assessing herbivory damage after the experiment was terminated, after six and twelve months. The data on bird and bat communities

(Chapter 1; Sam et al., 2019) collected at each elevation were correlated with the outcomes of the exclusion experiments.

In **Chapter 3**, I then examined the individual effect of bats on arthropod densities and herbivory damage on the foliage of understory trees at two lowland and two highland forest understories of the same elevational transect of Chapters 1 and 2. To separate the effect of bats from the effect of diurnal insectivores (i.e., birds), I established diurnal and nocturnal exclosures for one month.

In **Chapter 4**, I focused on the top-down control of flying vertebrates (i.e., birds and bats together, and birds and bats individually) on arthropods and herbivory damage in a temperate forest in Hokkaido, Japan. I employed the same methodology as that used in tropical sites (Chapters 2 and 3) using diurnal, nocturnal and permanent exclosures in the understory and expanding the permanent exclosures to the forest canopy. I accompanied the exclusion experiments with bird, bat, and ant surveys.

In **Chapter 5**, predator exclusion research was extended to various forests across different latitudes — encompassing warm, cold temperate, and tropical forests. Here, I only focused on diurnal and nocturnal exclosures to better understand the contribution of birds and bats individually on the trophic cascades across a large spatial scale. Consistent with other chapters, I complemented the results of the predator exclusion with surveys of predator communities combined with literature data.

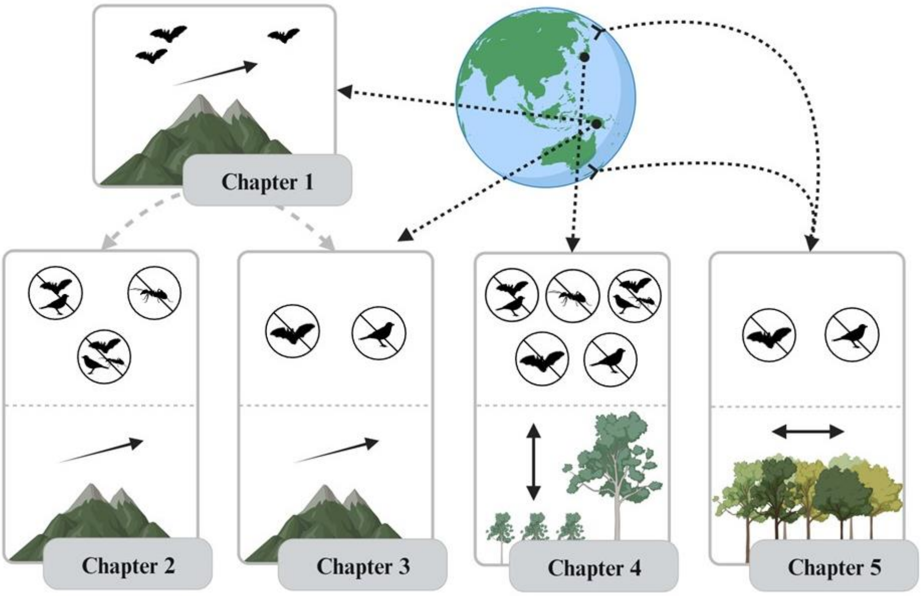

Figure 2: Graphical Thesis Outline: the upper part of the boxes indicates the predators excluded in the experiments of Chapters 2, 3, 4, and 5. The arrows in the bottom part of the boxes represent the types of comparisons—between elevations, strata, or latitudes. The dashed grey arrow means that Chapter 1 serves as a basis for Chapters 2 and 3. The world globe indicates the location of each project.

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2. Results

Chapter 1

Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea

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Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea

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Abstract

Over the past decades, elevational gradients have become a powerful tool with which to understand the underlying cause(s) of biodiversity. The Mt. Wilhelm elevational transect is one such example, having been used to study the birds, insects, and plants of Papua New Guinea (PNG). However, a survey of mammals from this forest elevational transect was lacking. We thus aimed to investigate patterns in the community structure and species richness of bats (Chiroptera) along the transect, link the species to available regional data, and explain the observed patterns by including environmental characteristics. Bat assemblages were surveyed between 200 m and a timberline at 3,700 m a.s.l. at eight study sites separated by 500 m in elevation. We conducted mist-netting and acoustic surveys to detect and identify species at each site. Regional data were compiled to compare local with regional diversity. Finally, biotic (i.e., food availability, habitat features) and abiotic (i.e., mean daily temperature) factors were included in our analyses to disentangle the ecological drivers underlying bat diversity. Results revealed that species richness decreases with ascending elevation and was best explained by a corresponding decrease in temperature. We observed both turnover and nestedness of the species composition at regional scale whereas turnover was dominant at local scale. Extensions and shifts of bat elevational ranges were also found in Mt. Wilhelm. Consequently, despite that the study was restricted to one mountain in PNG, it demonstrates how basic inventory surveys can be used to address ecological questions in other similar and undisturbed tropical mountains.

Introduction

Mountains are considered important biodiversity hotspots due to the great richness of endemic species that occur on them (Gradstein et al., 2008; Noroozi et al., 2018). They are also one of the most anthropogenically threatened environments in the world (Davis & Shaw, 2001; Ricketts et al., 2005). Consequently, elevational gradients are excellent systems for the study of biodiversity, global change, and conservation perspectives. Often used in models as a proxy for climate change, they allow us to study animal and plant responses to changes in biotic and abiotic factors (McCain & Colwell, 2011). Additionally, they can reflect responses to land-use changes, which often occur at low elevations (Becker et al., 2007). For these reasons, studies on assemblages, and especially of patterns of species richness along elevational gradients, have remained popular for many decades (Stevens et al., 2019). Several meta-analyses of terrestrial vertebrate groups have emerged in recent times that demonstrate varying trends in species diversity according to geographical location, largely because of their significant climatic differences (i.e., temperature, humidity) (e.g., McCain, 2005, 2007b, 2009, 2010).

Among terrestrial vertebrate groups, bats are considered commonly in studies of Holarctic (Piksa et al., 2013; Scherrer et al., 2019), Neotropical (Bogoni et al., 2021; Carvalho et al., 2019), and Afrotropical mountain ecosystems (Mongombe et al., 2019; Reardon & Schoeman, 2017). Two predominant patterns of bat species richness have been observed—a decrease with elevation in most tropical regions, and a unimodal trend in temperate regions (McCain, 2007b; McCain & Grytnes, 2010). The area hypothesis states that the amount of land area for each elevational band (e.g., 100–200m) on a mountain will be positively related to the diversity observed in that band (Terborgh, 1973), however, bats showed either no significant relationship or a negative association between species richness and available area (McCain, 2007a). It has been suggested that the highest bat species richness occurs in the elevational zone where water availability (e.g., precipitation, humidity) and temperature are simultaneously high (i.e., low and mid-elevations in tropical and temperate mountains respectively) (McCain, 2007b). Being small and volant, bats spend much of their energy budget on flight and thermoregulation, which is dependent on ambient temperature and therefore, limits their distribution in cold temperature regimes (Graham, 1983; McNab, 1982). In addition, water availability and temperature indirectly influence food resource availability (e.g., through fruiting tree phenology, the abundance of arthropods), and vegetation (e.g., shrub density), thereby influencing foraging behaviour and the availability of roosting sites (Charbonnier et al., 2016; Moura et al., 2016). While abiotic factors (i.e., temperature, available area within an elevation band) have been explored often in existing models, biotic factors as food resources and habitat characteristics have been considered rarely.

In addition to species richness, the species composition of bat assemblages can vary along an elevational gradient under different scenarios. It has been suggested that high-elevation bat species are able to exist at all elevations because of broad physiological tolerance and ecological requirements (Patterson et al., 1996). However, under a scenario of climate change, bat species are acclimated to high mountain conditions because they are geographically, ecologically, and/or physiologically constrained to high elevations (LaVal, 2004). Thus, species found only at high elevations are likely to expand their ranges and tolerate factors that limit lower-elevation species or be strictly constrained by recent events of climate change.

Exploring the different dimensions of β-diversity of bat assemblages may also explain the variations in species composition along environmental gradients. β-diversity can be partitioned into two components: turnover (i.e., replacement of some species by others between assemblages) and nestedness (i.e., species gain or loss between assemblages) (Baselga, 2010). If species are responding to environmental dissimilarities, spatial or historical constraints, then a greater turnover of species will be expected for study sites that have larger dissimilarity (Buckley et al., 2010). In contrast, nestedness may either reflect the quantity of niches available or occupied at the different study sites or be the result of extinctions or colonisations along the gradient (Ulrich et al., 2009). Studies that analyse the variation in the two components of β-diversity of tropical bat assemblages along elevational gradients are still sparse (Patterson et al., 1996; Presley et al., 2012; Turcios-Casco et al., 2021). The available results reveal that both turnover and nestedness of the bat assemblages can be observed along elevational gradient according to the geographical region.

Feeding specialization might be another factor affecting assemblage composition. Bat assemblages are typically dominated by insectivores, the relative species richness of frugivorous and nectarivorous bats peaks in the tropics, especially in the Neotropics, Oceania, and Australasia (Maas et al., 2016). However, patterns in the distribution of bat specialization along elevational gradients have rarely been documented, despite plant and insect distributions varying greatly. Fruiting trees are typically reported to decline in diversity and abundance with increasing elevation (Loiselle & Blake, 1991) while insects follow various patterns (i.e., none, peaking mid-elevation, decreasing, increasing) according to their group and/or localities (Hodkinson, 2005). Consequently, elevation might act as a filter of bat feeding guilds and impact the species composition of bat assemblages.

Papua New Guinean bats represent seven percent of the world's bat diversity (Bonaccorso, 1998; Mammal Diversity Database, 2021). From a total of 95 species, PNG has at least 19 endemic bat species (Bonaccorso, 1998). In recent decades, this unique richness attracted new research focused on viruses (Breed et al., 2010; Field et al., 2013), metabolism (McNab & Bonaccorso, 2001), and the home range of single species (Bonaccorso et al., 2002; Winkelmann et al., 2000, 2003). However, there is a lack of knowledge of bat community structure due to incidental focus within more encompassing mammal studies (Helgen, 2007; Helgen et al., 2011). Much of the effort for bat research in the past two decades has been as part of basic inventory surveys, environmental impact assessments and monitoring for industry

(Armstrong et al., 2020; Kale et al., 2018; K.P. Aplin and K.N. Armstrong unpublished reports), university research (Bonaccorso et al., 2002; Robson et al., 2012; Wiantoro, 2020) or else as part of biodiversity assessments for conservation organizations (Armstrong et al., 2015a,b; Armstrong & Aplin, 2011, 2014). While there is no central library of PNG bat echolocation calls, these studies have steadily accumulated knowledge and resources that support both acoustics-based and genetics-based identification, underpin recent species profile revisions in the IUCN Red List, and studies of taxonomic resolution (e.g., Wiantoro, 2020). They also mark a shift towards a primary reliance on acoustics-based detection and identification on field surveys, rather than trapping as was relied upon in the past, though trapping is still the best means of surveying for small species in the Pteropodidae and collecting vouchers to corroborate robust acoustics-based identification.

As a part of the Bismarck Range, Mt. Wilhelm is the highest peak in PNG (4,509 m a.s.l.) and offers a complete elevational transect in relatively intact tropical forests. Established study transects have become well-studied for birds (Marki et al., 2016; Sam et al., 2017, 2019), insects (Cesne et al., 2015; Finnie et al., 2021; Novotny et al., 2005; Orivel et al., 2018; Souto-Vilarós et al., 2020; Szczepański et al., 2018), and plants (Lofthus et al., 2020; Smith, 1977; Volf et al., 2020). Thus, given what previous efforts on other biota offer, the Mt. Wilhelm transect provided an opportunity not found elsewhere in New Guinea to study assemblages. Consequently, the present study aimed to: (a) document bat species richness patterns and species composition with increasing elevation to determine whether elevation is a filter of specific bat species and/or feeding guilds. We expected to see a steeply decreasing pattern in species richness, as it has been typically observed on tropical wet mountains; (b) investigate which of the abiotic (i.e., mean daily temperature) and biotic (i.e., habitat, food availability) factors drive bat diversity patterns and the changes in species composition along the transect. We assumed that temperature will best explain the patterns as described in the majority of past studies; (c) compare bat assemblages and their elevation ranges from the Mt. Wilhelm transect with the regional data (compiled from Bonaccorso, 1998) to determine which of the turnover or nestedness components of dissimilarity is the most important component of beta-diversity along elevations and, whether some species are out of their previously recorded ranges. We expected species turnover along the transect due to steep abiotic changes and that species we detect in highlands will have wider environmental tolerance, thus they will occur also in the lowlands, nevertheless, following the current scenario of climate change, we also expected to find species strictly constraint to high elevations.

Methods

Study area

We surveyed bat assemblages along the elevational transect of Mt. Wilhelm in PNG between 200 m and 3,700 m a.s.l. at eight elevational study sites separated by 500 m elevational increments (i.e., 200 m, 700 m, 1,200 m, 1,700 m, 2,200 m, 2,700 m, 3,200 m, and 3,700 m a.s.l. and ±60 m for each study site due to the rough terrain). The 30 km long elevational transect, which stretches between 5°44'S, 145°2'E and 5°47'S, 145°03'E, is located along the Bismarck Range's northern slope (Figure 1). Vegetation types used here follow Paijmans (1975): i.e., lowland alluvial forest (<500 m a.s.l.), foothill forest (501–1,500 m a.s.l.), lower montane forest (1,501–3,000 m a.s.l.), and upper montane forest (>3,000 m a.s.l.) (Figure S1.1 in Appendix S1 in supporting information). Mean daily temperature decreases linearly (r = -0.9) from 27.4°C at the 200 m a.s.l to 8.37°C at the timberline (3,700 m a.s.l) (Sam et al., 2019). The average annual precipitation is 3,288 mm (local meteorological station) in the lowlands, rising to 4,400 mm at the forest edge, with a distinct condensation zone between 2,500 and 2,700 m a.s.l. (Sam et al., 2019). Two seasons are recognised in PNG —a wet season from December to March and a dry season from May to October. However, there are only slight seasonal temperature variations in PNG and therefore it is generally hot and humid throughout the year (Vincent et al., 2015; Yule, 1996).

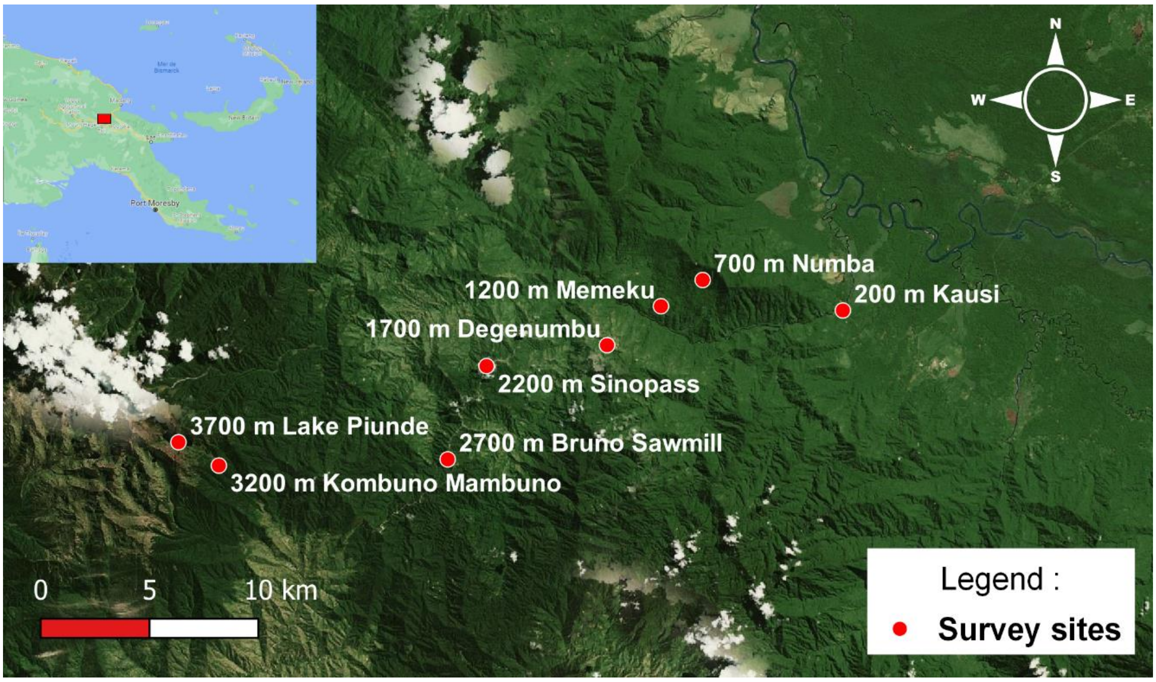

Figure 1: Map of the Mt. Wilhelm elevational gradient (source: Google earth; QGIS 3.12.2) and its location in Papua New Guinea (insert with red square).

Mist-netting and acoustic surveys

The bat assemblages were surveyed by mist-netting and by acoustic surveys, during two independent expeditions conducted in wet (February – April 2015) and dry seasons (June – July 2015). We used portable ultrasonic bat call detectors (Wildlife Acoustics EM3+ and a Pettersson Elektronik D240X connected to a Roland R-05 Wave/MP3 recorder) to record the calls of echolocating bat species. At each elevation, we surveyed the bats at five spots separated by 200 meters, visiting each of these spots for 15 minutes daily along a transect used in the previous study of bird communities (Sam et al., 2019). Surveys were conducted for four days per site from February to July 2015 after sunset (6 pm) but were only feasible for two days at 3,200 and 3,700 m a.s.l. (Table S2.1). Recordings were analysed by opening each WAV file in Adobe Audition version 22.0 and inspecting the spectrograms for bat echolocation pulses.

There were three different sampling rates in the data set: 22.05 kHz, 44.1 kHz, and 256 kHz. The characteristic frequency of echolocation pulses was determined after accounting for the sampling rate and was estimated from the power spectrum. Identification of bat species was undertaken in two steps. First, ‘echolocation call types’ were recognised from the recordings and defined based on a standardised naming scheme that has been used in many published and unpublished surveys across Papua New Guinea and Wallacea in recent years (Armstrong et al., 2020, 2015a, b; Armstrong & Aplin, 2011, 2014; Kale et al., 2018) and second, bat species identifications were attributed to each echolocation call type based on information from these and other surveys (annotated species list in Table S2.2, distribution of the species in Table S2.3 and illustration of call types in Figure S2.1). This two-step approach, along with the provision of illustrated examples of identified call types, provides transparency that allows for future verification of species identifications, and retrospective correction of species names on the basis of updated information. Nomenclature follows the current taxonomic and geographic database of bat species (https://batnames.org/).

We set a total of eight mist-nets (length x height: 15 x 3.5 m) at ground level in various habitat types per study site, including understorey ‘flyway’ spaces along human tracks, across creeks, and forest openings. We mist-netted five nights (12 hrs per night) per site in the wet season survey. During the dry season, we revisited elevations from 200 to 2,700 m a.s.l. only, and we operated the mist nets over four nights for five hours daily. We were not able to resurvey elevations above 2,700 m a.s.l. during the dry season due to logistical constraints. Mist-nets were moved to a new spot after every two nights. All mist-netted bats were identified to species using field guides by Bonaccorso (1998) and Flannery (1995) as well as (Irwin, 2017; Parnaby, 2009) for *Nyctophilus timoriensis* and *Nyctimene cyclotis* (Figure S2.2). However, morphologically similar *Paranyctimene raptor* and *P. tenax* could have been misidentified in the field; they can occur in sympatry, as previously observed by Bergmans (2001).

Regional data and explanatory variables

The regional data included only bat species described as present in Central Range and Sepik-Ramu Basin in Bonaccorso (1998). We summarized each bat species' elevational ranges described in the book (Table S3.1). The elevational ranges attributed to the bat species came from captures across the whole New Guinea. Nevertheless, it still reflects their tolerance to elevation even though some bat species are not found across the entire PNG area within their elevational range.

Temperature and humidity were recorded every hour for one year (April 2010–July 2011) using a data logger (Comet R3120) placed in the forest interior of each study site. We also measured the available land area of elevational belts 200 m wide across the whole New Guinea as a proxy for the land area for respective study sites (e.g., 100–300 m a.s.l., for the 200 m a.s.l. study site; measured in GIS software ARCGIS 9,3 and ERDAS ER Mapper 6). Mean annual temperature and available area decreased at a constant rate with elevation (Table S3.1), while mean humidity remained high across the entire transect (83.0%–97.4%) (Table S3.1).

We measured three variables related to habitat (Table S3.1) at 16 spots per elevational study site (128 in total, Sam et al., 2019): (1) Average canopy height (using a laser rangefinder; three measures/spot), (2) Shrub density (using a vegetation board (Lilith, 2007; MacArthur & MacArthur, 1961), five measures/spot, 1–3 m height), and (3) Canopy openness (5 photos/spot analysed with a Gap Light Analyzer; Frazer et al., 2001). These three variables define the vegetation structure at each site, which is the basis for the organization of bat foraging ensembles, defining flight spaces for foraging bats, and controlling the availability of roost sites (Charbonnier et al., 2016; Denzinger & Schnitzler, 2013; López-González et al., 2012).

In addition, we derived several predictors of food availability. Firstly, we used two food variables for frugivorous-nectarivorous bats (Table S3.1): (1) species richness and (2) abundance of fruiting trees (Villemant et al., 2016). Trees were counted and identified in three random plots of 20 x 20 m at each study site in the dry season of 2013. Further, we obtained the abundance and richness of the fruiting trees targeted by bats at each elevation by using plant genera recognized as having fruit or nectar consumed by pteropodid bats by the database of Aziz et al. (2021).

Moths (Lepidoptera) dominate the diet of most insectivorous species in PNG (Table S3.2). We used the (1) species richness and (2) abundance of Geometridae, one of the most important moth families (Beck et al., 2017; Vestjens & Hall, 1977) as an indicator of Lepidoptera availability. The specimens were collected using manual light trapping (May–August 2009; October–December 2009, January 2010) at all eight study sites of Mt. Wilhelm transect (Beck et al., 2017; Toko, 2011).

Statistical analysis

We used incidence data (i.e., presence/absence per sampling night) from the acoustic surveys as it was not possible to separate the vocalizations of individual bats. Mist-netting data were also converted to incidence data to facilitate comparison. We recorded the number of nights at a particular elevation when a given species was encountered. Considering that PNG is weakly seasonal, the dry and wet seasons were pooled in all analyses.

We used sample-based rarefaction to compare species richness by sampling days at each elevation (in EstimateS 9.1*;* Colwell, 2013) for both methods. Considering the short sampling period, we extrapolated the sampling effort by doubling the number of sampling days using the incidence-based richness estimator Chao2 implemented in the software EstimateS 9.1 (Colwell, 2013). It allows us to know how many sampling days we would need in the future to reach a plateau at each site in such a high diversity mountain. The sampling completeness of each site was also assessed to guarantee that compositional comparisons were based on reliable inventories. Sampling completeness was also estimated considering the values of the classic estimator Chao2 calculated separately for each site (using the software EstimateS 9.1) as the percentage of observed species against estimated species.

Captures (as a proxy of abundance from mist-netting data) and total species richness (from both methods) were also described for each of the three feeding guilds (frugivore-nectarivore, insectivore, frugivore-nectarivore-insectivore) described in (Bonaccorso, 1998). Capture rate was divided by the number of sampling days for consistency. To identify differences in capture rate between elevations, we ran an analysis of variance (ANOVA) and a Tukey's test of the capture rate per sampling day at each elevational study site.

We built a correlation map using the 'ggcorrplot' package (Kassambara, 2019) and calculated the significance of the correlations. Elevation, available area and mean daily temperature were highly correlated (R=1, Figure S4.1) and the mean humidity was constant along the transect. Thus, we used only the mean daily temperature as an abiotic predictor variable. In addition, we built an index of habitat complexity from the three habitat variables (i.e., canopy height, canopy openness and shrub density). Indeed, these three factors were highly correlated with each other (R>0.8, except shrub density), and the first axis of a principal component analysis (PCA) summarizing these variables was used as a predictor variable. The first PCA axis accounted for 33% of variation in habitat variables. Similarly, species richness and abundances of moths were highly correlated with each other (R=0.9, Figure S4.1) and the first axis of a principal component analysis (PCA) summarizing these two variables was used as a predictor variable. The first PCA axis accounted for 41% of variation in the moth variables.

Due to the small size of our dataset, only a limited number of variables could be incorporated into the models. First, we aimed to compare the effect of mean daily temperature and the effect of the habitat structure on bat species richness. Total species richness was used as the dependent variable in Poisson regressions with combinations of two predictor variables (log-transformed): mean daily temperature and the index of habitat complexity. Second, we aimed to compare temperature and food availability on partitioned species richness. Species richness partitioned into feeding guilds was used as the dependent variable with combinations of three variables (log-transformed): mean daily temperature, fruiting tree richness, and abundances, or the index of moth richness and abundance. We used ΔAICc and Akaike weights (w_1) to interpret regression results and evaluate models and their fits (Anderson & Burnham, 2002). Frugivore and nectarivore species were assigned to one main feeding guild in our models: frugivore-nectarivore. Frugivore-nectarivore-insectivore species (i.e., *Syconycteris australis*) was included into two guilds —the frugivore-nectarivore and insectivore guilds (i.e., its presence was included in two datasets). To determine the independent contribution of each explanatory variable to the response variable, we applied the hierarchical partitioning algorithm to our datasets using the 'hier.part' package (Walsh et al., 2008).

We used Mantel tests to disentangle the effect of mean daily temperature and habitat complexity on the compositional dissimilarity of bat assemblages. Three distance matrices were constructed: (1) a dissimilarity matrix of species composition by elevational study site using the Jaccard coefficient; (2) a Euclidean distance matrix accounting for temperature differences in elevation; and (3) a Euclidean distance matrix accounting for habitat complexity differences in elevation. We performed Mantel tests between bat composition and mean daily temperature, and between bat composition and the index of habitat complexity separately. The Pearson correlation method and 9,999 permutations were used by means of the 'vegan' package (Oksanen et al., 2013).

We produced heatmaps using the Jaccard dissimilarity index to compare bat species composition between sites using the 'vegan' package (Oksanen et al., 2013) in R software (R Core Team, 2020). The first heatmap was run using incidence data from both mist-netting and acoustic surveys. The second one was produced with regional data from Bonaccorso (1998) (i.e., bats from Central Range and Sepik-Ramu basin). We also performed a hierarchical cluster analysis using the Ward's Minimum Variance clustering with Jaccard dissimilarity index and built dendrograms. The contributions of spatial turnover and nestedness to the distribution pattern in our study were calculated using three beta diversity indices: Jaccard dissimilarity, nestedness-resultant fraction of Jaccard dissimilarity and the turnover fraction of Jaccard dissimilarity. These indices were calculated with the ‘beta.multi’ function of the ‘betapart’ package (Baselga & Orme, 2012). The significance of the observed nestedness and turnover values were tested using a null model with the quasi-swap method of the ‘oecosim’ function in ‘vegan’ package (Oksanen et al., 2013) in R. This method randomized species composition but keep the number of species within elevational sites constant. P-values produced by the statistic based on simulations informed us whether the observed turnover and nestedness values were significantly different from those expected by chance.

For screening patterns, elevational ranges of species were ranked by elevational midpoints, minima, maxima, then plotted as bar graphs, producing elevational ‘range profiles’ of the bat species found in Mt. Wilhelm and described in the regional data from (Bonaccorso, 1998). We used R statistical environment ((R Core Team, 2020), version 3.5.2) for all analyses.

Results

Species richness pattern

By mist-netting, we captured 701 individuals of 12 bat species (Table S2.3). We did not capture any individuals above 2,700 m a.s.l.. A total of 11 echolocation call types were recognised from the recordings, each of which can be associated with one or more bat species (Figure S2.1). From these, at least ten bat species in five families were recorded (i.e., confirmed) as being present on the survey (Table S2.3). In total, 21 species were observed in five months along the Mt. Wilhelm transect. This represents about 30 % of the regional species pool according to

Bonaccorso (1998). Species richness declined with increasing elevation, regardless of the survey method used or the data sources (Figure 2).

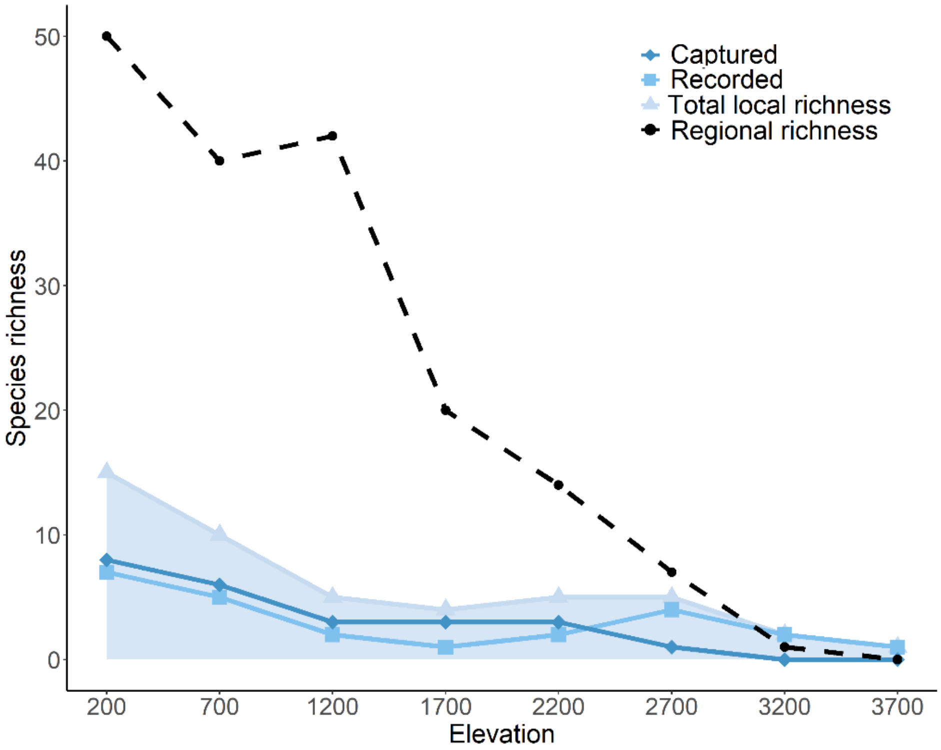

Figure 2: Bat species richness recorded from mist-netting captures, acoustic records, and both methods combined, at eight study sites of Mt. Wilhelm elevational transect in Papua New Guinea. Regional species richness according to Bonaccorso (1998).

The species accumulation curves did not reach the plateau during the acoustic surveys at 700 and 2,700 m by mist-netting at 700 m a.s.l. (Figure S4.2, a, b). On the other hand, the rarefaction curves showed that we quickly reached the highest level of species richness at high elevations (3,200–3,700 m a.s.l.) in both survey methods. However, by doubling the sampling days, stability was reached at all elevations, except at 700 m a.s.l.. Completeness analyses indicated that 92 % (ranging from 52 to 100%) of the estimated number of species was collected in average at each site using mist-nets. Using recorder, we however detected in average 85 % (ranging from 69 to 100%) of the estimated number of species (Table S2.1).

The mist-netting data revealed that the capture rate was rather constant along the elevational transect (Figure S5.1) except at 700 m a.s.l. where it was unusually high. Fruit-feeding bats were the most frequently captured (Figure S5.2), and *Syconycteris australis* dominated the samples (Table S2.3). However, in terms of the number of species, the richness of the frugivores-nectarivores and insectivores declined in a similar pattern along the transect (Figure S5.2).

Drivers of diversity

We first modelled total species richness with the mean daily temperature and an index of habitat complexity, followed by partitioned species richness (i.e., frugivore-nectarivore, insectivore) with the mean daily temperature and food variables. Selected according to AICc, the model with the mean daily temperature as a single variable performed better than any other combination (Table 1) regardless of the type of species richness. The hierarchical partitioning analysis showed that the independent effect of the habitat index closely followed the mean daily temperature (45 % and 55 % respectively) and confirmed that none of the food variables (i.e., fruiting trees and moths) significantly improved the model (Figure S6.1).

Table 1: Akaike's second-order information criterion (AICc) for multi-predictor models of observed bat species richness along the Mt. Wilhelm elevational transect, estimated for all bat observations and the observations partitioned into two feeding guilds. The bold text underlines the model which performed better than any possible combination.

All bats	$-\log(L)$	Akaike weight (w_1)	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$
Null	25.01	0.000	52.7	15.65
Temperature	**15.32**	**0.679**	**37.0**	**0.00**
Vegetation index	16.21	0.278	38.8	1.79
Temperature + Vegetation index	15.27	0.043	42.6	5.51
Frugivores-nectarivores	$-\log(L)$	Akaike weight (w_1)	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$
Null	17.446	0.002	37.6	12.53

Temperature	**9.31**	**0.884**	**25.0**	**0.00**
Fruiting tree abundances	15.65	0.002	37.7	12.67
Fruiting tree richness	16.54	0.001	39.5	14.46
Temperature + Fruit. tree ab.	9.28	0.055	30.6	5.55
Temperature + Fruit. tree rich.	9.30	0.054	30.6	5.58
Fruit. tree ab. + Fruit. tree rich.	12.51	0.002	37.0	12
Temp. + Fruit. tree rich. + ab.	9.21	0.001	39.8	14.74
Insectivores	$-\log(L)$	Akaike weight (w_1)	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$
Null	18.37	0.100	39.4	4.16
Temperature	**14.42**	**0.802**	**35.3**	**0.00**
Moth index	17.67	0.031	41.8	6.50
Temperature + Moth index	14.11	0.067	40.2	4.97

Mantel tests between bat composition and temperature, and between bat composition and the habitat index are both statistically significant (Mantel r: 0.68, p-value = 0.001, and Mantel r: 0.63, p-value = 0.007, respectively).

Assemblages of bats

The heatmap based on the Mt. Wilhelm data (Figure 3a) showed a rapid turnover of species along the elevation transect. We found high similarity between adjacent assemblages at the extreme ends of the transect, between 200 and 700 m and between 3,200 and 3,700 m but also at mid-elevation between 1,200 and 1,700 m a.s.l. The latter pair of sites shared the only species (i.e., *Miniopterus australis*) found at 3,700 m with a total of two species at 3,200 m a.s.l.. The cluster analysis identified a pronounced distinctiveness of low to high-elevation bat assemblages (200-2,700 m a.s.l.) from the highest ones (3,200-3,700 m a.s.l.) (Figure 3c). However, using regional data (Figure 3b), the heatmap revealed an increasing dissimilarity with increasing elevation. Assemblages also appeared similar between the closest sites (e.g., 200–700 m; 700–1,200 m a.s.l.) except for the highlands. The elevational distribution of bats ends at 3,200 m a.s.l. in regional data (Figure S3.1) so that the highest elevation (3,700 m a.s.l.) could not share any species with other sites. The cluster analysis revealed that the bat assemblages formed two clusters: one between 200 m and 1,200 m and a second one from 1,700 m to 3,700 m a.s.l. (Figure 3d).

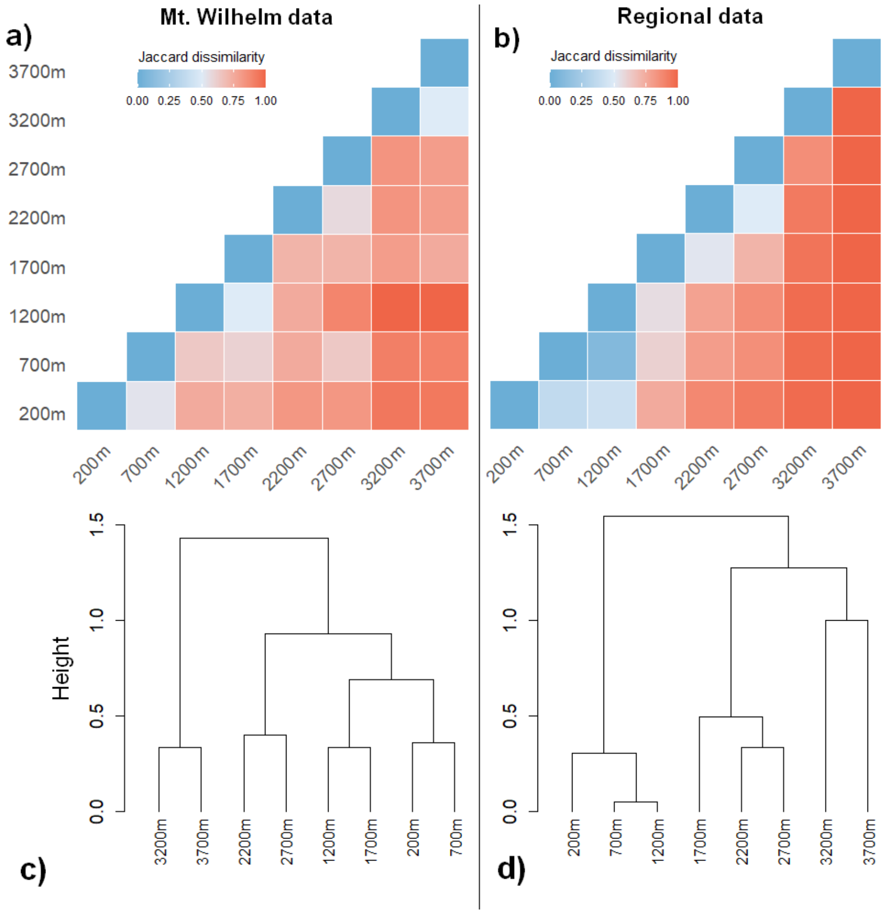

Figure 3: Heatmap of Jaccard dissimilarity index of local (mist-netted and acoustic data combined) bat assemblages found at Mt. Wilhelm (a) and potential bat assemblages based on the regional distribution of bats in Papua New Guinea (b). Dendrograms of the dissimilarity for the Mt. Wilhelm bat species (c) and for the regional dataset (d) built with Ward's Minimum Variance clustering with Jaccard dissimilarity index.

The complete multiple-site dissimilarity in species composition along the studied elevational transect was high (88%) and dominated by the turnover component (71%), whereas the value of the nestedness-related component was low (17%) (Table 2). However, using regional data, the complete multiple-site dissimilarity in species composition was high (86%)

being almost equally driven by the turnover component (46%) and the nestedness-related component (40%) (Table 2).

Table 2: Null model results of the multiple-site β-diversity components for species by site using the Mt. Wilhelm or the regional data. β-diversity components are represented by percentage (%) of total dissimilarity. Obs. (%)—percentage represented by β-diversity components of the total dissimilarity; Mean(sim)—mean values of the 9,999 simulations; 2.5%, 50% and 97.5%—the number of simulated values; p(sim)—p values.

	Obs (%)	Mean (sim)	2.5%	50%	97.5%	P(sim)
Species by site (Mt. Wilhelm data)						
Turnover	0.71	0.86	0.82	0.86	0.88	*<<0.001*
Nestedness	0.17	0.03	0.01	0.03	0.06	*<<0.001*
Species by site (Regional data)						
Turnover	0.46	0.87	0.85	0.87	0.88	*<<0.001*
Nestedness	0.40	0.01	0.007	0.01	0.02	*<<0.001*

Profiles of elevational ranges for bats in Mt. Wilhelm is dominated by the large number of species occurring in lowland habitats (76%) (Figure 4a). However, several species are found on the high montane slopes (above 2,200 m a.s.l.) that do not also occur in the lowlands. Similarly, using regional data, most bat species occur in the lowlands (88 % below 700), but several species found at mid-elevations (9%) present evidence of discrete elevational zonation (Figure 4b).

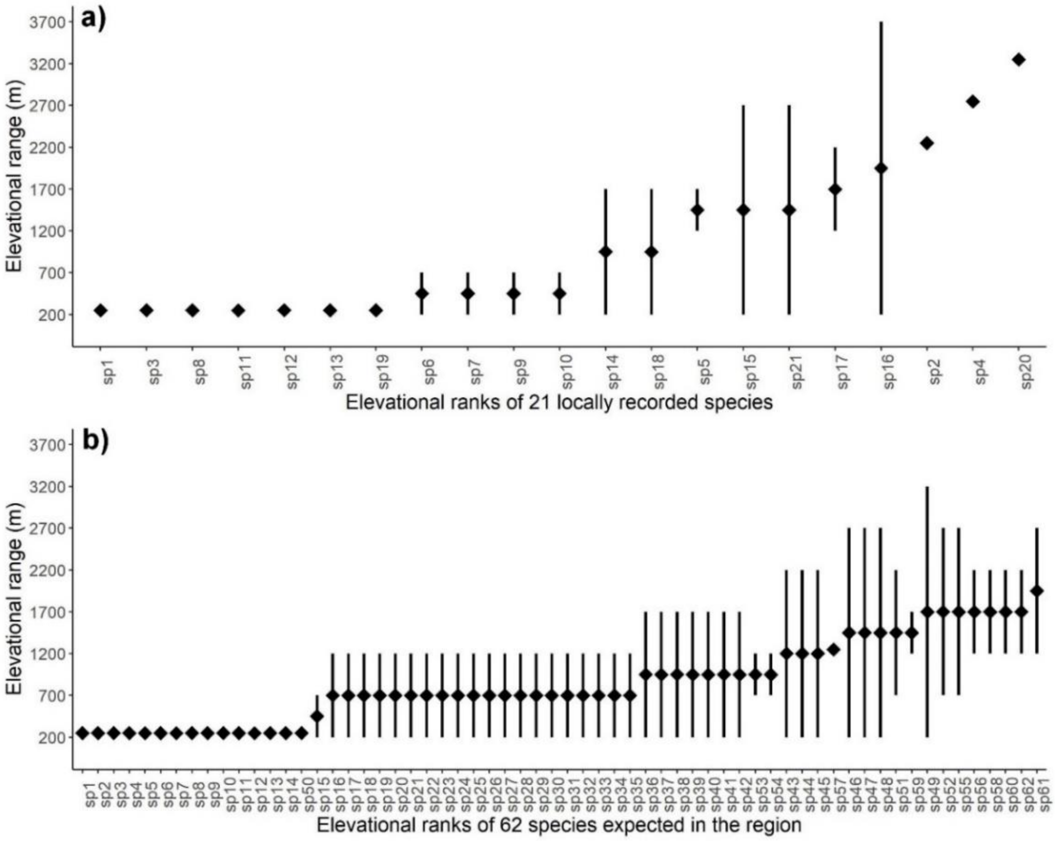

Figure 4: Elevational range profiles for the Mt. Wilhelm (a) and the regional dataset (b). Bars indicate the maximum and minimum elevational limits of each species' range, and species are ordered along the abscissa by ranked elevational midpoints.

Our results confirmed the upper elevation reported in the literature for most of the species at Mt. Wilhelm, apart from six species: *Hipposideros wollastoni, H. calcaratus, Dobsonia minor, Nyctimene draconilla, Paranyctimene raptor, Miniopterus australis* [=*Miniopterus* sp. 2 'small']), that were observed at higher elevations (Figure S7.1).

Discussion

Our study was the first detailed bat survey along a forest transect in PNG and revealed that Mt. Wilhelm hosts at least one-third of the bat species richness expected in that region (Bonaccorso, 1998), thus representing an important diversity hotspot. Bat species richness decreased with increasing elevation and the observed pattern was mainly driven by mean daily temperature. Species turnover described most of the species' distribution along the Mt. Wilhelm transect, while both turnover and nestedness were observed in the regional dataset. Our observations at Mt. Wilhelm showed that some bats were detected only at high elevations and seemed to be missing in the lower parts of their typical ranges. This pattern might be real or affected by incomplete sampling. Extensive studies are required to clarify this pattern and understand bat community structures in PNG.

Species richness pattern

Papua New Guinea is home to a very high number of bat species (95 species) and, with 36 pteropodid species (i.e., family Pteropodidae), boasts the second-highest diversity of Old World fruit bats in the world after Indonesia (Aziz et al., 2021). However, it is also one of the most data deficient and poorly-understood countries in terms of how the bat assemblages are structured with respect to their ecological roles (Aziz et al., 2021). Mt. Wilhelm represents a high diversity of bats with at least 21 species out of the 62 expected in that region. Our data indicate that more species would be revealed by a more intensive survey.

The decreasing species richness with increasing elevation followed the main decreasing pattern found in tropical mountains documented by McCain (2007). Even though the sampling completeness was relatively high regardless of the sampling method or the study site, the rarefaction curves showed that acoustic surveys would have to exceed eight days and coupled with all-night recordings from autonomous recorders to yield accurate numbers of species at 700 and 2,700 m a.s.l.. Furthermore, a recent study in the Neotropics revealed that the main centre of activity in bat species is in rainforest canopies (Marques et al., 2016), which has already been observed for birds in PNG (Chmel et al., 2016). However, since we did not survey bats at the canopy level due to logistical challenges, we potentially missed bats flying above the treetops, perhaps because our equipment could not detect the attenuated echolocation signals, or they were simply less likely to reach our understorey mist nets (Kalko & Handley, 2001; Marques et al., 2016). Our result underscored the necessity to employ both acoustic and capture methods in the forest canopy and understorey.

In terms of captures, we collected more frugivore-nectarivore individuals in the lowlands (i.e, 200–700 m a.s.l.) but we did not see significant differences in the capture rate from 1,200 to 2,700 m a.s.l.. This contrasts with studies in South American forests (Carvalho et al., 2019) where frugivores declined greatly above 1,000 m a.s.l.. At 3,200 to 3,700 m a.s.l., the habitats along rivers were mostly open (Figure S1.1 in Appendix S1), which made the captures more difficult, and our sampling effort was the lowest at those elevations. That is perhaps why we did not catch any bats above 2,700 m a.s.l.. However, we have no independent way of assessing catchability in the frugivorous species, in contrast with the insectivorous species for which we can detect them acoustically even though they are not easily captured. Therefore, we were unable to resolve whether frugivore-nectarivore are simply missing above 2,700 m a.s.l. due to environmental filters (e.g., fruit production, temperature) or whether it is the result of apparent mist-netting limitations.

Drivers of diversity

Despite using a range of factors including some rarely considered for bats (e.g., food availability), our analysis revealed that mean daily temperature have the strongest independent effect on bat species richness along the elevational transect, followed closely by the habitat index in explanatory power. Similar results were also revealed by the mantel test, showing that both temperature and habitat were driving the compositional dissimilarity of bat assemblages. As such, our data mirror those from other studies conducted in tropical mountains where temperature was also reported to be a strong correlate with bat diversity (McCain, 2007b) and species composition (Presley et al., 2012). Temperature could affect distributions through direct (e.g., physiology) or indirect effects (e.g., habitat, food resources) in different ways between feeding guilds. Mean daily temperatures were 9.9 and 7.9 ^{o}C at 3,200 and 3,700 m a.s.l. respectively, which is below the temperature tolerance of most bat species (Geiser & Stawski, 2011) and may explain why we did not capture any bats at these sites, and only recorded two species above 2,700 m a.s.l.. Besides, temperature could influence bat species richness indirectly through vegetation and food resources (Charbonnier et al., 2016; Moura et al., 2016). Indeed, the habitat complexity index (combining features of the vegetation structure) had also a strong independent effect on species richness. Vegetation structure could be important for bats, indirectly related to food resources, but also for roosting sites (Capaverde et al., 2018; Kunz, 1982; Perry et al., 2007). Roosting opportunities depend on the number of trees of appropriate size and whether or not they contain cavities or other structures appropriate for bats. Based on published data, 67 % of the species detected in Mt. Wilhelm potentially use foliage or tree hollows (Table S3.2). In contrast, the food variables had a very low effect on species richness of insectivores or frugivores-nectarivores. Insect abundance, and fruit and nectar production are all predicted to be low at high elevations (Loiselle & Blake, 1991; Terborgh, 1977). Studies suggest that the reduction in productivity with elevation (McCain & Grytnes, 2010) has a more substantial impact on fruit resources (e.g., figs) than on the other types of resources used by bats (e.g., insects) (Presley et al., 2012; Segar et al., 2017). The distribution of moths from Mt. Wilhelm shows a mid-peak pattern (Beck et al., 2017; Toko, 2011), which does not seem to be followed by insectivorous bats.

The inclusion of habitat features, fruiting tree and moth species richness, and abundances in the model did not change the relative level of influence of temperature on species richness. However, temperature, decrease linearly with increasing elevation while bat diversity does not. The steepest drop-off in numbers was between 200 m and 1,200 m a.s.l. and declining at a slower rate thereafter. It is thus likely that there are also other factors, that we did not consider (e.g., seasonal food availability), modifying the response by bats.

Assemblages of bats

According to regional data, dissimilarity kept increasing from similar assemblages in the lowest study sites (200–1200 m a.s.l.) to more dissimilar ones in the highest sites (1,700–3,200 m a.s.l.) with a clear disconnection of the assemblages between 1,200 and 1,700 m a.s.l.. The values of turnover and nestedness-related components of dissimilarity showed that both contributed to the distribution pattern of the bat species along the transect. Indeed, the assemblages of bats found at the highest sites were just a subset of bats from the lowlands, suggesting that the vast majority of the bat species found in this region are not restricted to mountainous areas. While some species at intermediate elevations were missing in low elevations and thus increased dissimilarity of the assemblages. However, potential identification issues and unresolved taxonomy might affect the understanding of species elevational distributions, especially in this long-standing regional dataset (Bonaccorso, 1998).

When the scale of the analysis was reduced, we found that species turnover had a large effect in determining beta diversity dissimilarity along the elevational transect of Mt. Wilhelm. Our study is the first bat survey conducted at the highest peak of PNG. We detected bats at the 3,700 m a.s.l. elevation band—never before recorded in PNG (Amick et al., 2021)—and observed wider bat ranges than the ones described previously for the region (Bonaccorso, 1998). These range extensions are most likely due to low sampling effort for bats at high elevations in PNG in the past, rather than any recent range expansions. In Mt. Wilhelm surveys, we found bat species at high elevations that were missing from the lowlands (*M. tristis/P. collinus, H. wollastoni, O. secundus*), which have been encountered more commonly at mid-high elevations. Globally, previous studies showed that the majority of bats found in highlands are primarily lowland species that occasionally commute to higher elevations when conditions become favourable (Patterson et al., 1996) or use these environments as commuting routes. Indeed, as previously mentioned, most bats are limited by direct and/or indirect effects of temperature, and life at high elevations could present an energetic challenge, especially for pregnant and lactating females (Kunz et al., 1995). In our sampling, low canopy openness in the lowlands could affect our ability to detect echolocation signals from bats flying over the canopy. Moreover, changes in call structure at high elevations have already been observed for one bat species (i.e., *Tadarida brasiliensis*) in a previous study (Gillam et al., 2009). Nevertheless, under a scenario of climate change, these bat species (i.e., *M. tristis/P. collinus, H. wollastoni, O. secundus*) may have been recently constrained to high elevations because of spatial elements and/or their ecology and/or physiology. However, we are unable to resolve whether we likely missed these species in the lowlands because of the use of methods that have a greater bias towards the detection of species below the canopy or whether these bat species spanning only in high elevations are the consequences of acclimations to climate change. Extensive surveys with a greater level of effort might help to answer this question.

Conclusion

Mt. Wilhelm provides habitat for a globally significant bat fauna whose species richness follows the typical decreasing pattern with elevation found in other tropical mountains. Mean daily temperature explained the vast majority of this pattern, however, we suspect that additional factors (i.e., seasonal food availability) could improve the models. Bat assemblages also varied gradually along the elevational transect, as we describe for the first time for PNG. The fact that six species in this study were recorded above their typical elevational range, including some detected above the previously described maximal distribution for PNG, might be the result of climate change or basic survey issues and lack of good quality historical data. A greater level of effort would shed light on this, which is potentially important, as the bats of PNG remain largely understudied. This study highlights how the results of basic inventory surveys that employ a comprehensive, multi-method effort for bat sampling can be used to address ecological questions that might help with impact assessments.

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Authors contributions

PKA conducted the fieldwork, recorded bat calls, and mist-netted the bats; KNA and ES performed bat call identifications; ES performed data analyses, extracted data from literature and wrote the first draft of the manuscript; KS designed and funded the study and helped with the analyses; PKA, KNA, KS, and VN contributed significantly to revisions.

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.ns1rn8pww (Sivault et al., 2022).

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Supporting information

Appendix S1

Figure S1.1: Pictures of the different habitats along the Mt. Wilhelm elevational gradient A : Kausi (200 m) ; B : Numba (700 m) ; C : Memeku (1200 m) ; D : Degenumbu (1700 m); E : Sinopass (2200 m); F : Bruno Sawmill (2700m); G : Kombuno Mambuno (3200 m); H : Lake Piunde (3700 m).

Appendix S2

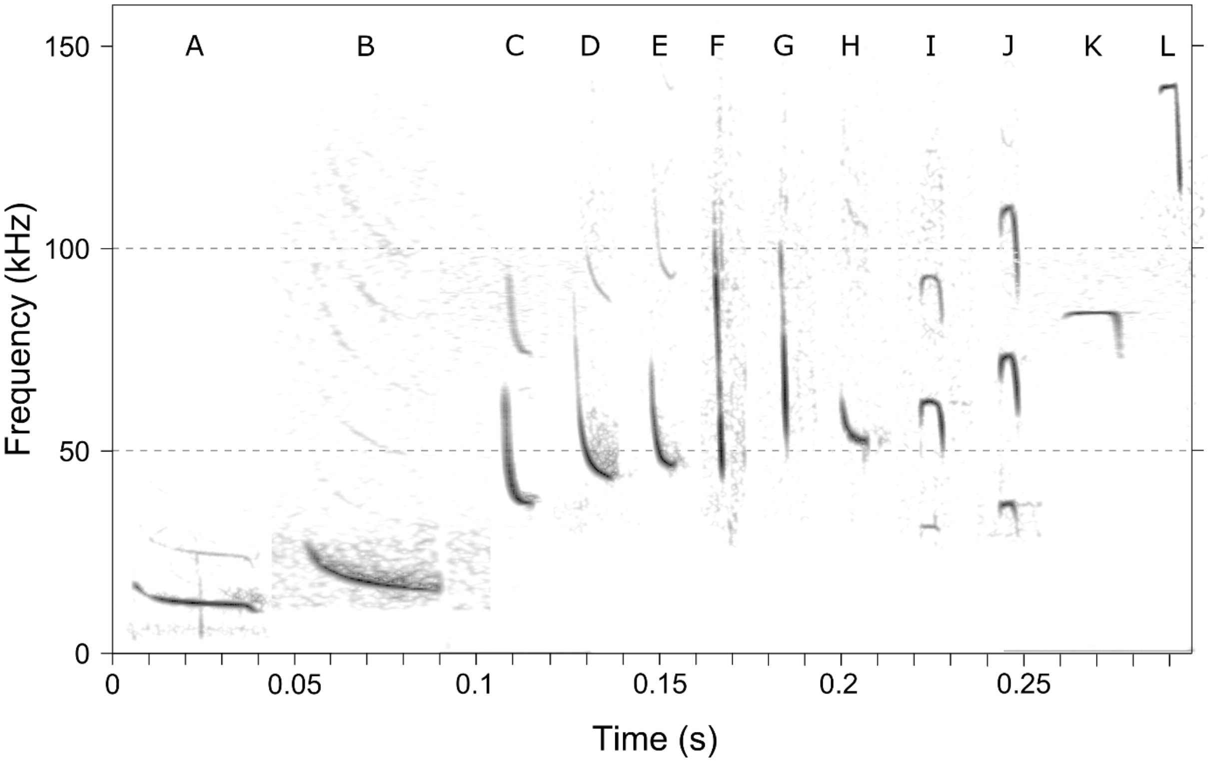

Figure S2.1. Representative echolocation pulses of the call types recognised and species identified (**A**: *13 cFM Austronomus kuboriensis*; **B**: *18 cFM Otomops secundus*?; **C**: *38 st.cFM Miniopterus tristis grandis / Pipistrellus collinus*; **D**: *43 st.cFM Miniopterus* sp. 1 'medium'; **E**: *48 st.cFM Pipistrellus papuanus.*; **F,G**: *45-50 bFM Nyctophilus microtis*; **H**: *54 st.cFM Miniopterus* sp. 2 'small'; **I**: *62 i.fFM.d Emballonura beccarii / Mosia nigrescens*; **J**: *72 i.fFM.d Emballonura beccarii / Mosia nigrescens*; **K**: *84 mCF Hipposideros wollastoni*; **L**: *140 sCF Hipposideros cervinus*; time and frequency axes for each pulse have been adjusted to be equivalent).

Figure S2.2: Pictures of the bat species captured using mist nets (source: P. Amick). A: *Dobsonia minor;* B: *Hipposideros calcaratus;* C: *Macroglossus minimus;* D*: Miniopterus australis;* E: *Nyctimene aello;* F: *Nyctimene albiventer;* G: *Nyctimene certans*[1]*;* H: *Nyctimene draconilla;* I: *Nyctophilus microtis;* J*: Nyctophilus shirleyae*[2]*;* K: *Paranyctimene raptor;* L: *Syconycteris australis.*

[1] Previously *Nyctimene cyclotis* (Irwin 2017)

[2] Previously *Nyctophilus timoriensis* (Parnaby 2009)

Table S2.1: Summary of the sampling completeness of the Mt. Wilhelm mist-netting and recording surveys. n= number of sampling days; n(spots)=number of spots where bats were recorded (using one single recorder) or captured (corresponding to 8 mist-nets); n(transect)=number of transects settled at each study site; So=number of species observed; Se= number of species estimated from the Chao2 estimator; Cm= sampling completeness calculated as So/Se * 100.

	Recording						**Mist-netting**					
Sites	n	n(spots)	n(transect)	So	Se	Cm	n	n(spots)	n(transect)	So	Se	Cm
200m	4	5	1	7	7.13	98%	9	8	1	8	8.44	94.7 %
700m	4	5	1	5	9.5	52.6%	9	8	1	6	8.67	69 %
1,200m	4	5	1	2	2.38	84.0%	9	8	1	3	3.44	87 %
1,700m	4	5	1	1	1	100%	9	8	1	3	3.89	77 %
2,200m	4	5	1	2	2	100%	9	8	1	3	3.9	76 %
2,700m	4	5	1	4	6.25	64 %	9	8	1	1	1.15	86 %
3,200m	2	5	1	2	2.25	88 %	5	8	1	0	0	100 %
3,700m	2	5	1	1	1	100 %	5	8	1	0	0	100 %

Table S2.2 Annotated species list provided to justify identifications and range extensions, with references additional to the main list.

EMBALLONURIDAE Sheath-tailed bats

Beccari’s sheath-tailed bat *Emballonura beccarii meeki*

and/or

Lesser sheath-tailed bat *Mosia nigrescens papuanus*

Echolocation call types: *62 i.fFM.d* and *72 i.fFM.d*

The echolocation call types *62 i.fFM.d* and *72 i.fFM.d* are attributable to *E. beccarii* and *M. nigrescens*, but associating each call type with each species is currently not possible. Both species have a similar elevational range, and a geographical range that includes, or has the potential to include, the study area (Bonaccorso 1998; Armstrong 2021a,b). In addition, these two species have around the same body size (Bonaccorso 1998) and therefore an expected overlap in the range of the characteristic frequency of the strongest, second harmonic of the call. Association of these two call types with a capture is the best way to provide an unambiguous identification. In the analyses, the echolocation call types *62 i.fFM.d* and *72 i.fFM.d* are considered as two species.

HIPPOSIDERIDAE Leaf-nosed bats

Fawn leaf-nosed bat *Hipposideros cervinus*

Echolocation call type: *140 sCF*

This echolocation call type is typical of *H. cervinus* (Armstrong et al. 2020). No faint fundamental frequencies were evident in the examples recorded.

Wollaston’s leaf-nosed bat *Hipposideros wollastoni*

Echolocation call type: *84 mCF*

This call type was identified to *H. wollastoni* based on the similarity of the characteristic frequency and the relatively long pulse duration to reference call examples associated with captures from elsewhere (K.N. Armstrong unpublished data). This record extends the geographic range of the species as it is represented by the IUCN Red List (Armstrong and Aplin

2021). *H. wollastoni* is one of few hipposiderids that can be encountered commonly at mid-elevations (e.g., Bonaccorso 1998: up to 2,000 m asl; Armstrong and Aplin 2011: 1,600 m asl; Armstrong et al. 2015a: up to 1,900 m asl, probably misidentified therein as *H. muscinus*, incorrect upper elevational limit cited from this study by Armstrong and Aplin 2021; Armstrong et al. 2020: 1,400 m asl). The record from the present study extends the known elevation range of the species (Bonaccorso 1998) by around 200 m.

VESPERTILIONIDAE

Papuan Pipistrelle *Pipistrellus papuanus*

Echolocation call type: *48 st.cFM*

Distinguishing the echolocation calls of *Pipistrellus* from those produced by species of *Miniopterus* is often quite difficult, but the increasing frequency of the terminal portion of pulses can be a feature that allows attribution to *Pipistrellus*. In this case, given distribution records (Bonaccorso 1998), *P. papuanus* is the most like source, but the New Guinea Pipistrelle *P. angulatus* is also a possibility, as is the unidentified bent-winged bat *Miniopterus* sp. 1 'medium'. Capture is required to provide an unambiguous identification of the source of this call.

Papuan Long-eared bat *Nyctophilus microtis*

Echolocation call type: *45-50 bFM*

The most likely source of this call type is a species of long-eared bat, and *N. microtis* is the most commonly encountered species at relatively low elevations (Bonaccorso 1998; K.N. Armstrong unpublished data) where it was recorded on the present survey. Another possibility are clutter calls of a species of *Pipistrellus* or *Miniopterus*, which can be difficult to distinguish from calls of *Nyctophilus* spp. if call quality is relatively low. Capture is required to provide an unambiguous identification of the source of this call.

MINIOPTERIDAE Bent-winged bats

The entire Indo-Australasian radiation of Miniopteridae was recently revised by Wiantoro (2020), though the names applicable to species in Papua New Guinea have yet to be published formally. The present survey recorded three echolocation call types that can be attributed to a species of *Miniopterus*. Indo-Australasian *Miniopterus* can be categorised into three groups based on overall body size, and representatives of two or more size groups are typically found together throughout the Indo-Australasian region. Until formal publication of names for Papua New Guinean *Miniopterus*, and until follow up capture and DNA barcoding for identification can be undertaken in the study area, reference to the echolocation call types encountered there can be considered more appropriate than species names. Applicable names that might have been attributed in the past are discussed for each echolocation call type.

Greater Melanesian Bent-winged Bat *Miniopterus tristis grandis*

or

Mountain Pipistrelle *Pipistrellus collinus* (Vespertilionidae)

Echolocation call type: *38 st.cFM*

This echolocation call type has two possibilities for its source. One is the larger-bodied bent-winged bat species *Miniopterus tristis grandis* that has been recorded as high as 2,700 m asl previously based on capture and genetic evidence (Armstrong et al. 2020). Alternatively, it could be attributable to *Pipistrellus collinus* given previous records of the species as high as 2,800 m asl (Bonaccorso 1998). Reference calls of *P. collinus* are unavailable. Trapping is required to resolve the identification.

Unidentified bent-winged bat *Miniopterus* sp. 1 'medium'

Echolocation call type: *45 st.cFM*

This species would have been referred to as either *Miniopterus macrocneme, M. medius* or *M. schreibersii* in the past, which have a geographic range that includes the study area (Bonaccorso 1998; Armstrong et al. 2021a,b). The name *M. schreibersii* is no longer used for Indo-Australasian *Miniopterus* (Tian et al. 2004), with the name *M. orianae* used commonly for the taxon on the Australian continent that is also found in New Guinea (e.g. Churchill 2008; Jackson and Groves 2015). The ‘moderate’ characteristic frequency of the echolocation calls is typical of this body size type on the Papua New Guinea mainland, being at least 5 kHz higher on average than larger-bodied species.

Unidentified bent-winged bat *Miniopterus* sp. 2 'small'

Echolocation call type: *54 st.cFM*

This echolocation call type is known to be from a small-bodied bent-winged bat species, which is currently referred to as *Miniopterus australis* in Papua New Guinea (Armstrong et al. 2021c). It is encountered commonly, including at higher elevations (Armstrong and Aplin 2011: 2,900 m asl; Armstrong et al. 2015a: up to 1,900 m asl, possibly misidentified as *Pipistrellus collinus* therein; Armstrong et al. 2020: 2,700 m asl).

MOLOSSIDAE Free-tailed bats

Mantled Free-tailed Bat *Otomops secundus*

Echolocation call type: *18 cFM*

The species name given here is a suggested attribution of this echolocation call type given that there is no reference call information from either of the two *Otomops* species in Papua New Guinea. The harmonic profile of the call is typical of a molossid, and the characteristic frequency is too high for *Austronomus kuboriensis*. Further, the high elevation of the record precludes its attribution to *Chaerephon jobensis*, a species of *Ozimops* or *Otomops papuensis* (based on elevation ranges in Bonaccorso 1998). Other records of calls from mid-elevations attributed to *O. secundus* are from unpublished biodiversity surveys (Armstrong 2021c); and some call types suggested to be from *O. secundus* are of slightly higher frequencies than were recorded in the present study (e.g., Armstrong et al. 2015a: 25 kHz; Armstrong et al. 2020: 30 kHz). The nearest confirmed geographic record of *O. secundus* is Tapu, on the Upper Ramu River Plateau, Madang Province (Bonaccorso 1998).

New Guinea Free-tailed bat *Austronomus kuboriensis*

Echolocation call type: *13 cFM*

Austronomus kuboriensis is the only species of bat in Papua New Guinea that emits an echolocation call that has a characteristic frequency of the fundamental as low as 13 kHz. This species has a recorded in the elevational range between 1,900 and 2,800 m asl (Bonaccorso 1998). The single pulse detected in the present study at 700 m could be incorrect, since it is common to see low frequency signals not attributable to bats resembling echolocation calls in bat detector recordings (K.N. Armstrong pers. obs.), but the quality and pulse characteristics certainly provide reasonable evidence. This elevational record would need to be confirmed with a sequence of pulses.

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Table S2.3: Bat species captured (MN in Call type column) and acoustically recorded along the Mt. Wilhelm gradient. Grey zones underline bat species captured and recorded as well. Numbers indicate the number of individuals captured. Blue zones underline the bat species elevational ranges previously described in Bonaccorso (1998). Note that call types not attributed to a specific species, or more than one species have no blue zones. Diet information comes from Bonaccorso (1998). See Fig. S2.2 for illustration of echolocation call types.

Species	**Call type**	**200**	**700**	**1,200**	**1,700**	**2,200**	**2,700**	**3,200**	**3,700**	**Food**
HIPPOSIDERIDAE										
Hipposideros wollastoni	*84 mCF*					X				Insects
Hipposideros cervinus	*140 sCF*	X								Insects
Hipposideros calcaratus	*MN*		1							Insects
EMBALLONURIDAE										
Emballonura beccarii / Mosia nigrescens	*62 i.fFM.d*	X	X	X	X					Insects
Emballonura beccarii / Mosia nigrescens	*72 i.fFM.d*	X								Insects
VESPERTILIONIDAE										
Pipistrellus papuanus	*48 st.cFM*	X								Insects
Nyctophilus microtis	*45-50 bFM + MN*	X	1	X						Insects
Nyctophilus shirleyae	*MN*	1								Insects
MINIOPTERIDAE										
Miniopterus tristis / Pipistrellus collinus	*38 st.cFM*							X		Insects
Miniopterus sp. 1 'medium'	*43 st.cFM*	X	X			X	X			Insects
Miniopterus australis [=*Miniopterus* sp. 2 ‘small’]	*MN + 54 st.cFM*	X	X		1	1	X	X	X	Insects
MOLOSSIDAE										
Austronomus kuboriensis	*13 cFM*		X				X			Insects
Otomops secundus?	*18 cFM*						X			Insects
PTEROPODIDAE										
Syconycteris australis	*MN*	79	211	89	136	78	19			Fruit/ Nectar/ Insects
Macroglossus minimus	*MN*	2	5							Nectar
Paranyctimene raptor	*MN*	22	5	6	1					Fruit
Nyctimene albiventer	*MN*	27								Fruit
Nyctimene draconilla	*MN*	3								Fruit
Nyctimene aello	*MN*	4								Fruit
Nyctimene certans	*MN*			1		1				Fruit
Dobsonia minor	*MN*	4	1							Fruit

Appendix S3

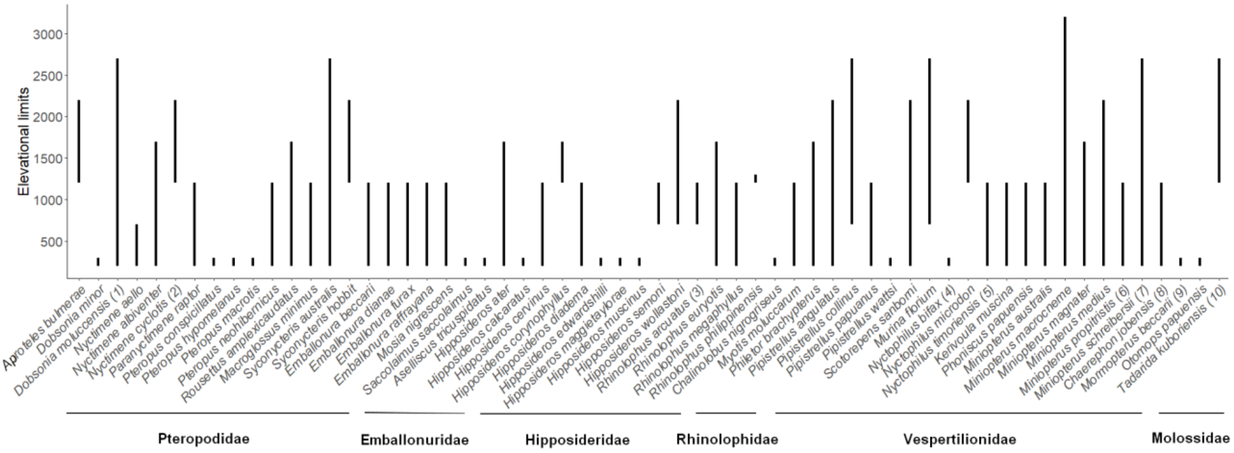

Figure S3.1: Regional data on elevational distribution of bats after Bonaccorso (1998; with reference to updated nomenclature below the figure).

[1]*Dobsonia magna* (Simmons & Cirranello 2022) *;* [2]*Nyctimene certans* (Irwin 2017) *;* [3]*Rhinolophus mcintyrei* (Patrick et al. 2013) *;* [4]*Nyctophilus bifax is no longer in PNG* (Parnaby 2009)*;* [5]*Nyctophilus shirleyae* (Parnaby 2009)*;* [6]*Miniopterus tristis* (Simmons & Cirranello 2022)*;* [7]*Miniopterus orianae* (Jackson and Groves 2015)*;* [8]*Mops jobensis* (Gregorin & Cirranello 2016)*;* [9]*Ozimops beccarii* (Jackson and Groves 2015)*;* [10]*Austronomus kuboriensis* (Gregorin & Cirranello 2016).

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Table S3.1: Explanatory variables and GPS location at each site along the Mt. Wilhelm. F.tree ab= Fruiting tree abundance; F.tree sp= Fruiting tree richness; Moth ab= Moth abundance; Moth sp= Moth richness.

Sites	Temp. (°C)	Humid. (%)	ShrubD	CanopyH	CanopyO	Area (log)	F.tree.sp	F.tree.ab	Moth sp.	Moth ab.
200 m	24.5	97.4	8.4	50.5	11.7	2.1	14	27	201	2311
700 m	22.3	94.2	19.4	44.2	15.2	1.6	24	33	239	1805
1,200 m	19.4	95.7	40.1	42.3	16.2	1.4	30	59	391	2194
1,700 m	18.3	94.9	40.1	42.3	16.2	1.3	23	80	402	3903
2,200 m	15.6	97.7	38.3	32.2	40.3	1.1	18	77	305	2631
2,700 m	13.1	99.3	28.4	40.1	40.5	0.9	17	66	197	1134
3,200 m	9.8	93.9	38.3	19.2	21.2	0.6	16	82	181	2091
3,700 m	7.8	83.0	20.4	13.4	98.2	0.3	6	27	37	355

Table S3.2: Roosting and foraging information found in Bonaccorso (1998; using current nomenclature) for the species detected on Mt. Wilhelm.

Species	Caves	Trees	Buildings	Foraging	Diet
HIPPOSIDERIDAE					
Hipposideros wollastoni	x			NA	NA
Hipposideros cervinus	x	x	x	Gleaner and aerial in dense forest and urban areas	Beetles, moths
Hipposideros calcaratus	x			NA	NA
EMBALLONURIDAE					
Emballonura beccarii	x			Gleaner, clear or dense forest, next to streams	Beetles
Mosia nigrescens	x	x	x	From canopy to ground level from forest to urban areas	Aerial and foliage-clinging insects, ants
VESPERTILIONIDAE					
Pipistrellus papuanus		x	x	Urban and open areas	Aerial insects
Pipistrellus collinus	NA	NA	NA	Native gardens	Aerial insects
Nyctophilus microtis	x	x		NA	NA
Nyctophilus shirleyae		x		Gleaner, subcanopy and over water	Moths and beetles
MINIOPTERIDAE					
Miniopterus tristis	*x*			Above canopy, clear areas	Aerial insects
Miniopterus australis	x	x		Beneath the canopy	Aerial insects
MOLOSSIDAE					
Austronomus kuboriensis	NA	NA	NA	Hawking above canopy	Beetles
Otomops secundus	NA	NA	NA	Open areas, canopy and urban areas	Large insects, beetles
PTEROPODIDAE					
Syconycteris australis		x		Generalist	Moraceae, Piperaceae, Solanaceae, flowers, insects
Macroglossus minimus		x	x	Generalist	Pollen, nectar
Paranyctimene raptor		x		Gardens, swamps	Ficus, Piper
Nyctimene albiventer		x		Ground or around trees	NA
Nyctimene draconilla		x		Fresh swamp, river	Fruits
Nyctimene aello		x		Subcanopy	Figs
Nyctimene certans		x		Ground and subcanopy	Maybe figs
Dobsonia minor		x		Dense understory	Figs, piper

Appendix S4

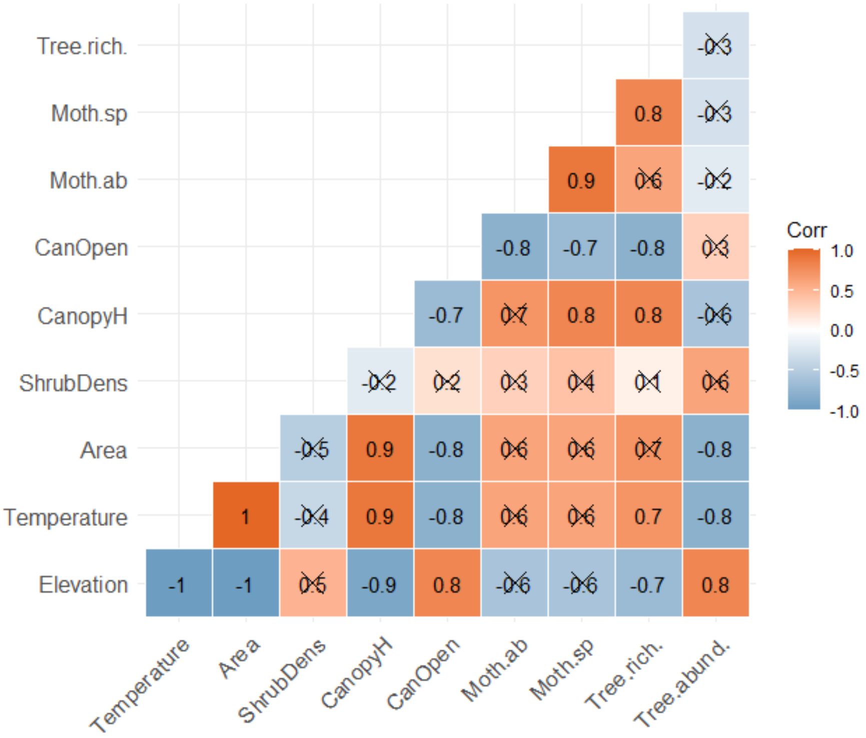

Figure S4.1: Correlation table of all the explanatory variables used in the models. Dark red means a very high positive correlation between two variables. The values correspond to the R coefficient between two variables. A cross means that the correlation is not significant. CanopyH= Canopy height; CanOpen= Canopy openness; ShrubDens= Shrub density; Tree.abund= Fruiting tree abundance; Tree.rich. = Fruiting tree richness; Moth.ab= Moth abundance; Moth.sp= Moth richness.

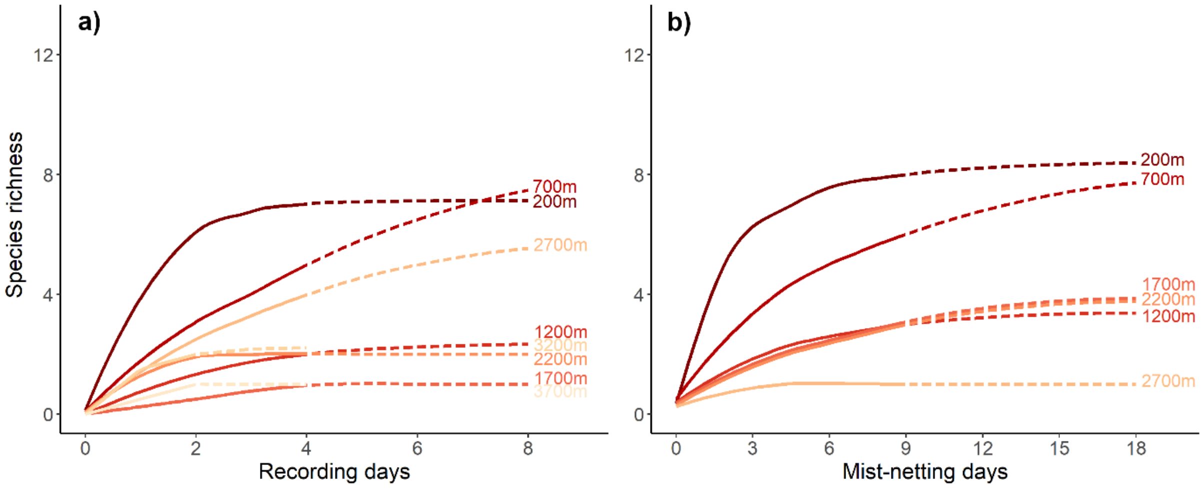

Figure S4.2: Rarefaction curves of observed and extrapolated (dashed lines) (days x2) number of bat species according to the number of recording (a) or mist-netting days (b) along the elevational transect of Mt. Wilhelm in Papua New Guinea.

Appendix S5

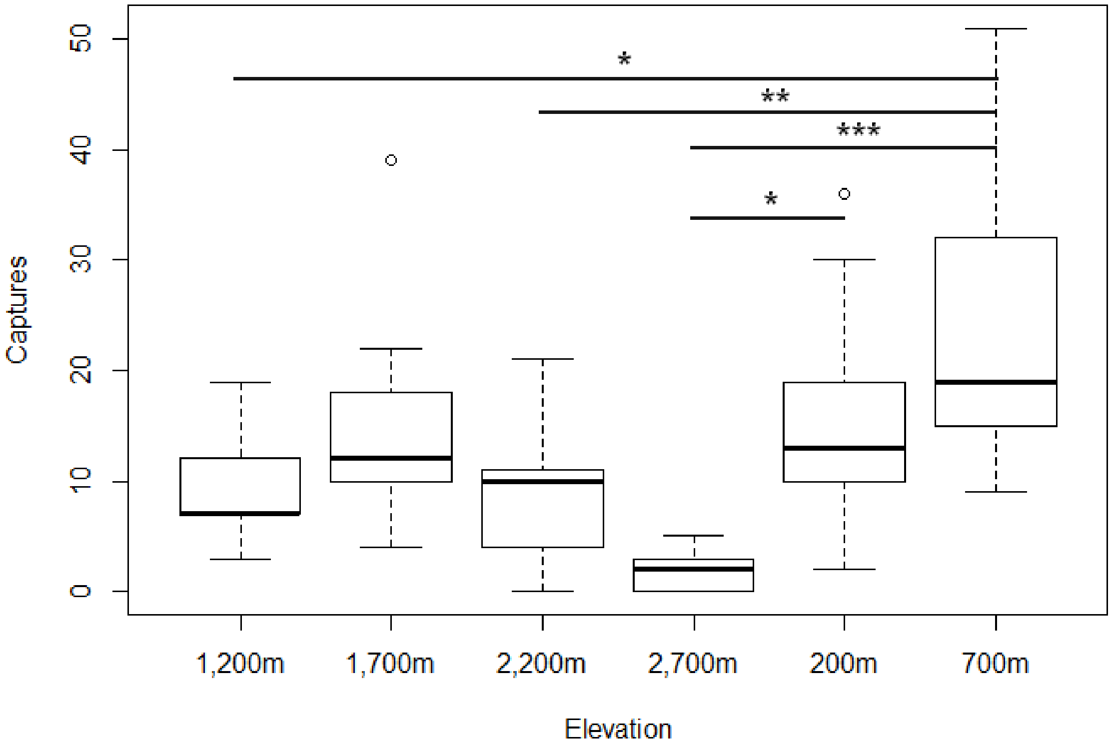

Figure S5.1: Boxplot of the capture rate/sampling day at each elevational study site from mist-netting surveys in Mt. Wilhelm. * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, NS P > 0.05.

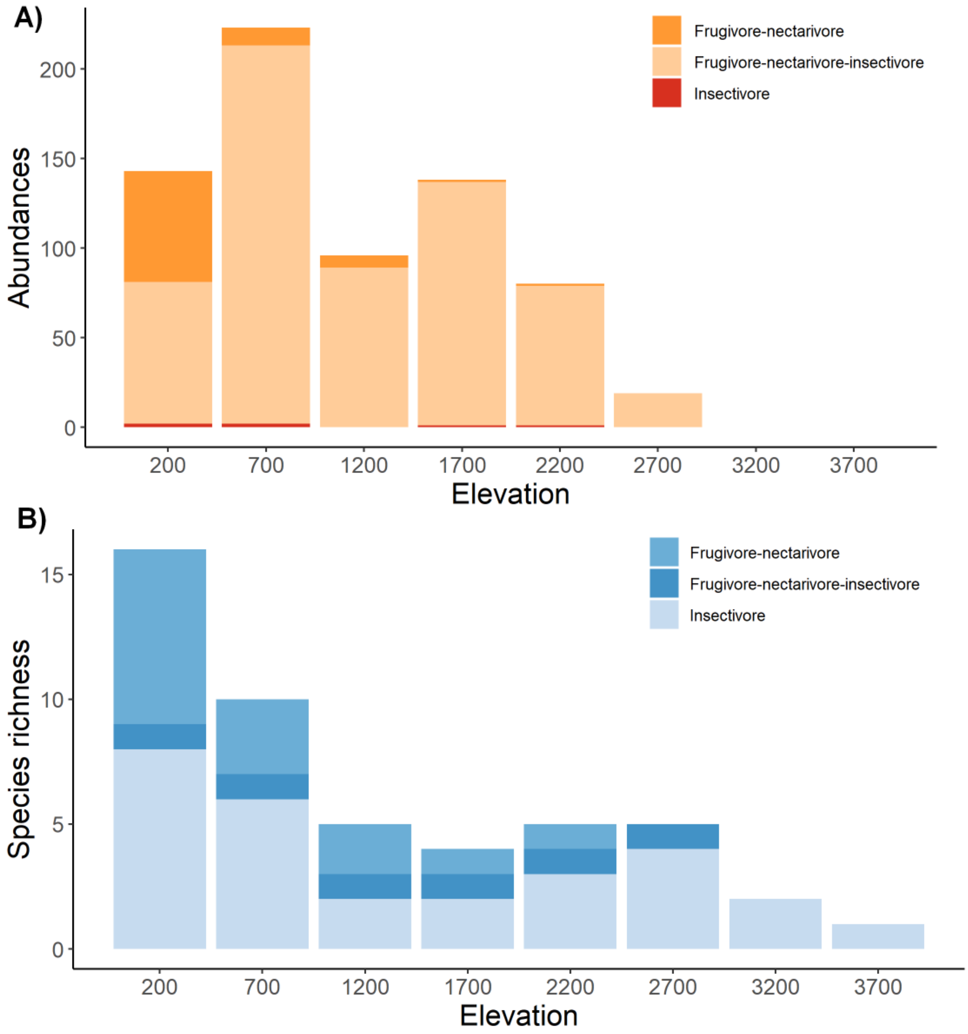

Figure S5.2: A) Bar chart representing bat captures partitioned in three feeding guilds along the elevational gradient of Mt. Wilhelm from mist-netting data. B) Bar chart of the total species richness partitioned in three feeding guilds along the elevational gradient of Mt. Wilhelm from acoustic and mist-netting data.

Appendix S6

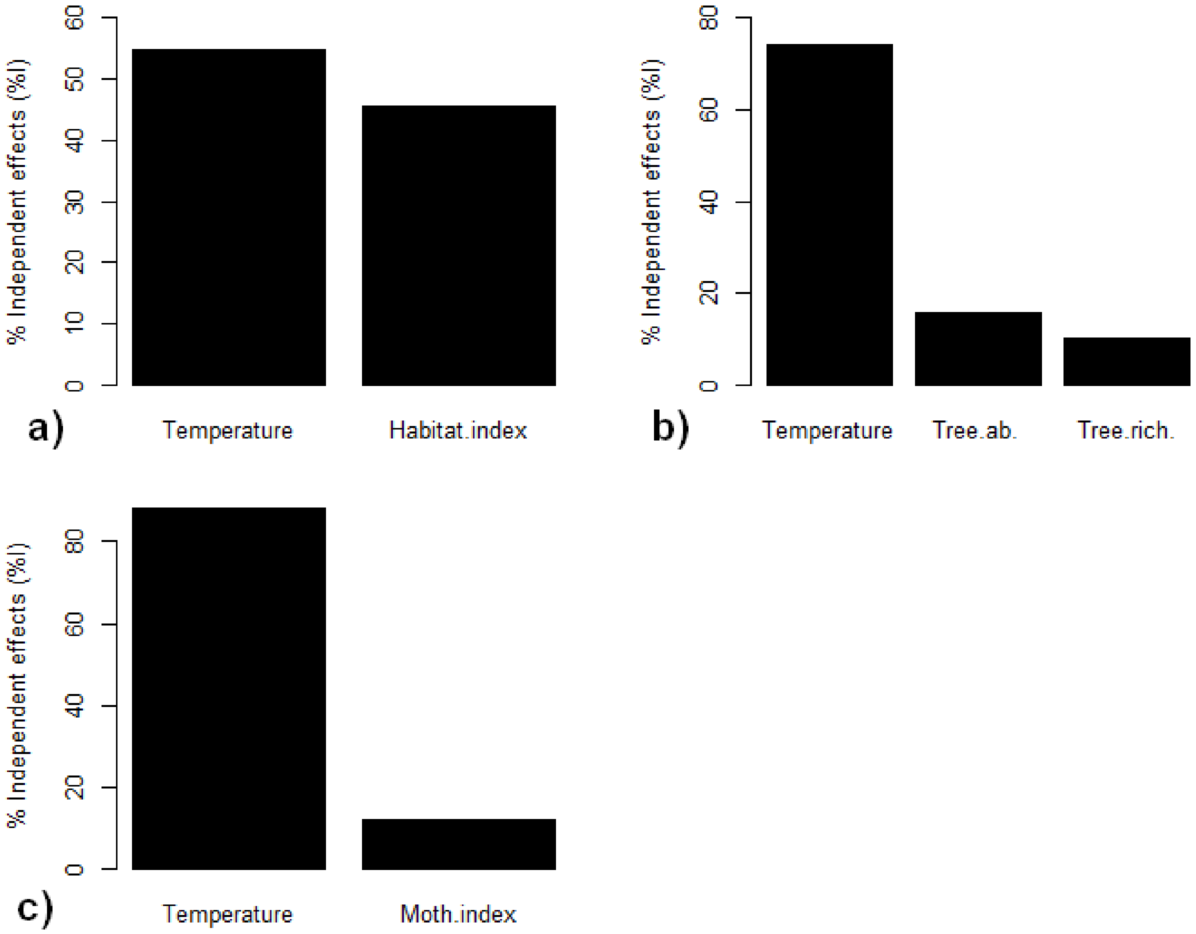

Figure S6.1: Hierarchical partitioning of the predictors of the total species richness (a), frugivorous-nectarivorous species richness (b) and insectivorous species richness (c).

Appendix S7

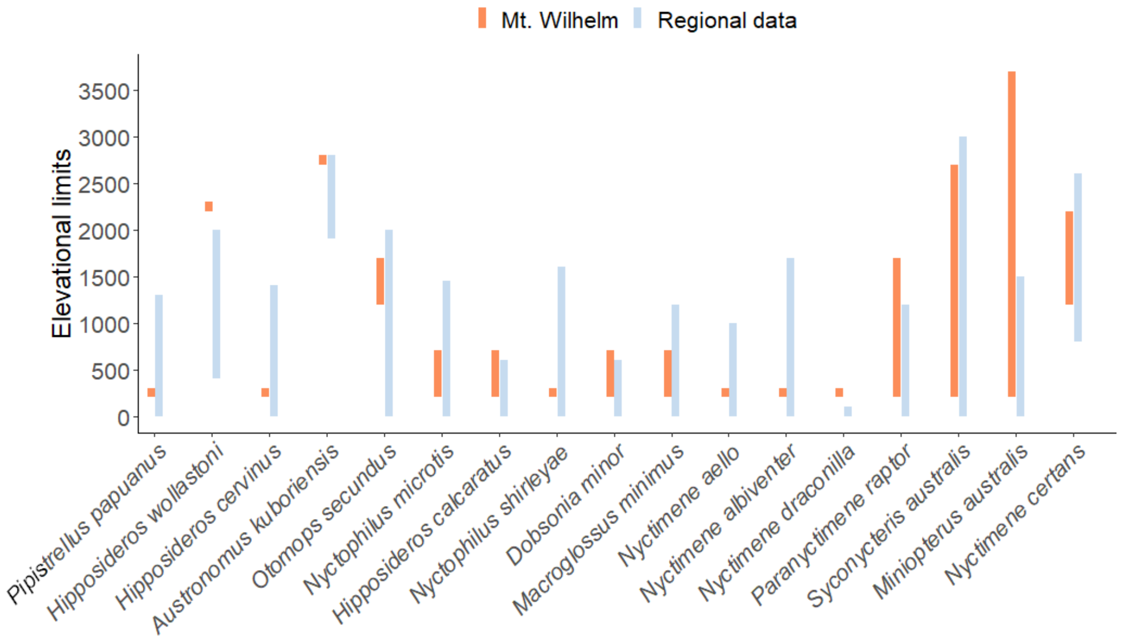

Figure S7.1: Comparison of the elevational ranges of the bat species found in Mt. Wilhelm with regional data (Bonaccorso 1998). Note that calls attributed to none, or more than one species are not presented here.

Chapter 2

Vertebrates, but not ants, protect rainforest from herbivorous insects across elevations in Papua New Guinea

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Vertebrates, but not ants, protect rainforest from herbivorous insects across elevations in Papua New Guinea

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Abstract

Aim: The effects of insectivorous predators on herbivorous prey should have a cascading effect releasing herbivory pressure and favouring plant's biomass. However, it remains unclear whether different types of predators regulate herbivores to the same degree across seasons, and how their interactions affect lower trophic levels across elevations where predator communities differ significantly. Therefore, we investigated the impact of excluding flying vertebrate predators and ants (individually and in combination) on arthropods and herbivory across tropical seasons along a rainforest gradient spanning 3,500 m a.s.l..

Location: Papua New Guinea

Taxon: Multi-taxon

Methods: We excluded predators from 560 saplings in two six-month-long predator exclusion experiments, controlling for seasonality. Saplings were spread across 8 sites, evenly spaced at 500 m elevational increments from 200 to 3,700 m a.s.l.. We measured change in the abundance of arthropods and herbivory damage and analysed them by linear and generalised linear mixed models.

Results: Exclusion of flying vertebrate predators, but not ants, led to a significant increase in both arthropod density and herbivory damage. The density of arthropods increased significantly by 37% when flying vertebrates were excluded and by 33% when both flying vertebrates and ants were excluded. Both season and elevation significantly influenced this effect. Leaf damage increased significantly by 50% in exclosures of flying vertebrates alone and by 36% in combined exclosures of flying vertebrates and ants. In contrast, the exclusion of ants alone had no significant effect on arthropod density or leaf damage, which increased by 12% and 9% respectively, although the effect decreased with increasing elevation.

Main conclusions: The overall effect of flying vertebrate predators on arthropod density and leaf damage remains consistently strong along the whole elevational gradient. In contrast, ant driven trophic cascades were detected only in lowland. Disappearance of insectivorous flying vertebrates could lead to substantial negative consequences for plants.

Introduction

Insect herbivores are the primary consumers of plant leaf tissue in tropical forests (Coley and Aide 1991, Coley and Barone 1996, but Suzuki, et al. 2013), and their impact is notably increased in the absence of top-down control (Mooney, et al. 2010, Sam, et al. 2022). This top-down control is therefore a high-value ecological service across a range of tropical ecosystems (Schmitz 2006, Sekercioglu 2006). It is usually assumed that different insectivorous predator groups have similar effects and are thus treated as a single functional unit, leaving their individual or joint effects largely unknown (Mooney 2007, Perfecto and Vandermeer 1996, Richards and Coley 2007, Sih, et al. 1998). Different predator groups may differ in their contributions to the number, type and size of prey consumed. Resolving the often-complex trophic dynamics of multiple types of predators in the same community and their cascading effect on plant performance remains an important challenge in ecology (Singer, et al. 2017). This challenge is primarily rooted in the variable strength of trophic cascades between predators, prey, and plants both within (Moon and Stiling 2004, Mooney and Linhart 2006) and between communities (Shurin, et al. 2002).

Birds and bats, and to a lesser extent terrestrial insectivorous vertebrates, consume large quantities of arthropods (Kalka and Kalko 2006, Mooney, et al. 2010, Nyffeler, et al. 2018). They are likely to act as intraguild predators, feeding both on predatory as well as herbivorous arthropods (Ingala, et al. 2021, Karp and Daily 2014, Milne, et al. 2016, Sam, et al. 2017), with a preference for large arthropod prey (Kaspari and Joern 1993). The impact of insectivorous birds on lower trophic levels has been shown in some but not all studies (Mooney, et al. 2010, Van Bael, et al. 2008). In some studies, the impact of bats on herbivorous arthropods was shown to be comparable to birds (e.g., Kalka and Kalko 2006, Williams-Guillén, et al. 2008). Despite this, bats are often erroneously overlooked in exclusion studies (Mooney, et al. 2010, Sam, et al. 2022), as the typical approach of covering foliage with a net effectively quantifies the combined effect of excluding both 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 important predators of arthropods in certain habitats (Hölldobler and Wilson 1990, Rosumek, et al. 2009). However, their general predatory significance remains equivocal despite extensive research on their value as natural enemies of pests and agents of biological control agents (Mestre, et al. 2012, Philpott and Armbrecht 2006, Rosumek, et al. 2009, Way and Khoo 1992). It remains mostly unknown whether ants feed on predatory and herbivorous arthropods in equal proportions (Singer et al. 2017), and thus whether they have the capacity to distort trophic cascades. However, as predation is body-size dependent, ants feed on prey which is typically smaller than the prey of vertebrates (Remmel et al. 2011). Previous efforts have failed to detect the effect of ants on lower trophic levels or have shown temporal inconsistency (Tanhuanpää, et al. 2001, Sam, et al. 2022). Plant damage in the absence of ants varies considerably, with a reported increase between 0 and 250% on average. These increases are significantly affected by both the duration of the ant exclosure (Sam, et al. 2022), and the productivity of the study site (Rosumek, et al. 2009, Sam, et al. 2022). Ant exclosures are difficult to conduct (Hood, et al. 2022, Rosumek, et al. 2009) 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 accurately measure the realized top-down control and trophic cascade to plants from ants.

Different predator groups favour not only specific prey types but also different sizes. As predator size also determines preferred prey sizes, we can also expect the effect of predators to alter the mean body size of insect communities. For example, the mean size of caterpillars was

12% smaller on saplings where birds were not excluded through preferentially feeding on large caterpillars (Singer, et al. 2017). Similarly, birds and bats were shown to reduce the mean body size of Araneae, Formicidae and arthropod larvae (Karp and Daily 2014). In contrast to vertebrate predators, ants are expected to hunt smaller prey. Therefore, there will be a much higher abundance of smaller insects in ant exclosures and therefore mean body size would be smaller.

Predator communities are not uniform across time and space. Variations in the diversity and abundance of animal taxa along elevational gradients lead to changes in the relative importance of predator groups at different sites on the same gradient (Camacho and Aviles, 2019, Colwell, et al. 2016, McCain 2005, Rahbek 1995, Sam, et al. 2019). As such, elevational gradients provide an excellent experimental environment for studies focussing on the individual and combined effects of insectivorous predators on prey and plants (Schemske, et al. 2009). As climate change is expected to lead to further changes in predator distribution and ecosystem function (Chen, et al. 2011), it is increasingly important to understand the effects of various groups of predators along large environmental gradients, while accounting for the environmental and seasonal factors affecting these interactions.

Given the differential nature of different predator groups on prey communities, different predator groups may have a differential cascading effect on herbivory. Here we, therefore, investigated the impact of flying vertebrate predators and ants (individually and in combinations) on arthropod communities and leaf herbivory along a 3,500 m tropical forest gradient in Papua New Guinea. We aimed to answer the following questions: (1) Do predators, individually and in combination, significantly affect the density of arthropods along the elevational gradient? We hypothesise that the removal of predators will result in increased arthropod density on plants and that the effect will be both independent and additive, as flying vertebrates may also consume ants (Sam, et al. 2017). (2) Are the effect of ants and vertebrate predators detectable on the mean body size of arthropod communities? We propose that arthropods will be relatively larger in the absence of vertebrate predators and relatively smaller in the absence of ants. (3) Do any of the predator groups display disproportionate impacts on the densities of predatory and herbivorous arthropods? We expect that both focal predator groups (i.e., flying vertebrate predators and ants) act as intraguild predators whereby they feed on both herbivorous and predatory arthropods, similarly, thus diminishing the effect of trophic cascades but not enough to make in undetectable. (4) Does the effect of predators cascade down to the trophic level of plants, and does it elicit detectable changes in herbivory damage? Considering our first hypothesis, we suggest that the removal of predators will have a measurable effect on plants thus resulting in increased herbivory.

Materials and methods

Study sites and experimental trees

Our study was conducted 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).

We conducted predator exclusion experiments on tree saplings. As there is no single tree species or genus that is distributed along the complete elevational gradient, we chose to work predominantly with *Ficus* saplings which represent the most dominant and ecologically important genus between 200 and 2700 m a.s.l. We had to work with other locally dominant species at the two highest elevations (Table S1). Prior to the experiment, we selected and tagged saplings from the appropriate species. We selected 80 (or 40 at 3,200 and 3,700m asl) individual saplings per elevational study site (8 in total), i.e., 560 saplings along the entirety of the elevational gradient (Table S2). The number of tagged species at each site ranged from 3 – 7 and most of the 18 tree species occurred in multiple elevational study sites. For statistical 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. Additionally, trees containing ant nests or with abnormally high herbivory or fungal damage were excluded. The selected tree species did not produce any exudates or sugar droplets that attract ants. Average leaf sizes of the selected species ranged from 16.31 to 154.10 cm^2 (mean ± S.E. = 52.16 ± 6.12). The mean sapling DBH at the beginning of the experiment was 1.16 cm for exclosures and 1.17 cm for controls.

Experimental design

We prevented flying vertebrate predators (i.e., birds and bats together but for example not lizards, VER) from accessing 20 out of the 80 preselected saplings at each elevational site between 200 and 2,700 m a.s.l. We also prevented ants from accessing another 20 saplings (ANT) and both flying vertebrate predators and ants accessing another 20 saplings (ALL) at each elevation. We left 20 saplings without predator protection as controls (CON). At the elevational sites 3,200 and 3,700 m, we protected 20 saplings against vertebrates (VER) and kept 20 as control saplings (CON). There were no ant exclosures at these two sites as they are above the natural elevation range of ants (Moses 2015, Colwell et al. 2016).

To exclude flying vertebrates (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 with a total volume of 10 m^3, which enclosed an average of 1.63 (± S.D. 1.02) m^2 of leaf area. The exclosure materials did not attract arthropods, did not significantly affect access of arthropods to foliage, did not damage leaves or branches, and did not significantly reduce light. We attached a system of ropes to neighbouring vegetation (i.e., strong branches) in order to secure the exclosures in place (thus preventing the exclosure from moving and disturbing the foliage of the target saplings). Observations confirmed that netting did not exclude small lizards as they were seen crawling under the cage. However, one ca. 50 cm long lizard was found tangled in the netting and was subsequently released, suggesting the exclosures partially prevented access to 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 strip 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 plant hollows. The ants foraging on foliage were removed by both beating and manual removal. We placed tuna baits (one teaspoon under a gauze tied to the trunk of the tree) 20 cm above the Tanglefoot layer and checked for the presence of ants two hours later, to confirm that ants are absent. 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 our analysis excluded all ant exclosure saplings where ant activity exceeded 3 ants on a single checking date (3 saplings in total). Tangle foot might negatively affect activity of other crawling insects, but not those which fly or jump on the foliage directly. It has been regularly used in ant exclosures studies (e.g., (Morris et al. 2015; Philpott et al. 2014). Ant removal was successful. There was a total of 538 and 884 ants found on control saplings (CON) and on saplings protected against vertebrates (VER) respectively, but only 13 and 30 on saplings protected against both types of predators (ALL) and ants only (ANT) respectively, 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 in ANT and ALL saplings.

To exclude all (ALL) predators (ants and vertebrate predators) we used a combination of the above methods, i.e., by applying Tanglefoot to the trunk, installing a cage around the sapling, and preventing the foliage from touching the cage. Tanglefoot was also applied to all of the support ropes used to lower the cage and hold it in place to prevent ants from accessing the sapling via neighbouring vegetation.

Measured variables

First, we assessed the effect of exclusion experiments on arthropod densities. We sampled the effect of predator exclusion after 6 and 12 months, corresponding to the dry and wet seasons respectively (Table S2). We carefully opened the protective netting where needed. The trunk of the sapling was then slowly lowered above a 2x2m mosquito net, wrapped into the net, and sprayed by fast knock-down insecticide (Mortein® Fast Knockdown Aerosol Multi Insect Killer). Shortly after we shook the foliage firmly, opened the net, collected all arthropods (>1mm) and preserved them in vials filled with DNA-grade ethanol. All arthropod individuals were later identified into orders or families and measured to the nearest 0.1 mm, life stage and feeding specialization were also recorded (Table S3). The insecticide’s residues can be detected on surfaces for up to 90 hours in indoor conditions (Mortein® product safety specification), thus the application was unlikely to have an effect on the second survey conducted 6 months later.

Second, we assessed herbivore-induced leaf damage which occurred during the experimental exclusion of predators, we randomly selected two small branches (ca. 50 leaves in total) and collected all their leaves at the beginning of the experiment. We estimated how many other leaves in total were present on the sapling and used this number to calculate the total leaf area (from which we just collected arthropods). We took photographs of the ca. 50 flattened leaves of each sapling against a 50 x 50 cm^2 white background. Using Adobe Photoshop CS6 (Adobe Systems Inc., USA), we outlined the missing edges of the leaves based on their 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) for each individual leaf. We then estimated the percentage of leaf–area loss per m^2 of foliage. Using the count of the number of leaves, we calculated the total leaf area of each sapling (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, with the only difference being that *all* foliage was now collected from each sapling. We placed all leaves collected from an individual sapling into a bag, randomly selected ca. 50 leaves for photographing and further analyses, and weighed all leftover foliage as well as the leaves used for photography. This allowed us to calculate the 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 and check for potentially overlooked arthropods. We then confirmed that leaf herbivory within a branch (i.e., herbivory on leaves from the first survey) was closely correlated to herbivory on leaves randomly collected within the whole plant (i.e., herbivory on leaves from the first survey; $P < 0.001$, $R = 0.854$). Further, the estimated leaf area (from the first survey) was significantly correlated ($P < 0.001$, $R = 0.358$) to the real leaf area based on leaf weight (from the second survey).

Predator survey

We assessed predator abundance and species richness using data from long-term monitoring efforts in the area. Specifically, we surveyed bird communities repeatedly by point counts to assess species richness and relative abundance, with this methodology and data published in several studies. In short, 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. Species richness and relative activity of bat communities were surveyed in the understory during two expeditions conducted in wet (February – March 2015) and dry seasons (June – July 2015). This method and data were published in Sivault, et al. (2022). In short, 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 metres at each elevation, in line with the bird transect methods described above. Surveys were conducted for four days per site after sunset (6 pm).

We assessed relative ant abundance by hand collection at each of the study sites. The trunk of each sapling was inspected for ants at breast-height for 10 minutes, and also by the tuna bait method in May-June 2014. More details on the respective surveys of predators are provided in the Supplementary material in the section Additional methods and lists of species are in Tables S4 and S5.

Data analysis

Arthropod densities: We used a linear mixed model and model selection to determine the effect of our experimental treatments on arthropod densities. We used arthropod density (per m^2 of leaves) 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 elevational trends and included in interactions. We used tree species as a random effect in our model to account for differences in baseline arthropod densities between species. Individual saplings were used as a second random factor as each of the 560 focal saplings was surveyed twice i.e., in both wet and dry seasons. As each sapling has a unique code and belongs to a given species, sapling identity is intrinsically nested within plant species. Thus, even though both were run as separate random effects, they act as nested.

Body sizes: We calculated the mean body size of arthropods from each of the saplings in each season, and we used the same model as described above for arthropod density. The response variable was the mean body size of arthropods found on each sapling in the given season and the data were not transformed.

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

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, $\bar{Y}_{I-}$) and control group (in the presence of insectivorous predators, $\bar{Y}_{I+}$) and was thus calculated as ($\ln[\bar{Y}_{I-}/ \bar{Y}_{I+}]$) for each of the three treatments at each elevational study site and season. We then constructed linear models, selected the best one, and used the function *get_model_data* from package 'metan' to obtain effect estimates (https://github.com/KatkaSam/GRAD_Exclosures).

Relative abundance (and activity for bats), 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. The number of saplings with ants on them and the abundance of ants on baits were correlated with the log response ratio LRR of the ant exclosure treatment at each elevation. All data were normalized on the scale of 0-1 and averages across both seasons were taken as the data from the predator surveys did not perfectly synchronize with the exclusion experiment.

Results

Change in arthropod densities

After the removal of predators, the density of arthropods was generally higher and increased more in the wet season than in the dry season (Figure 1, Table S6). Based on the model predictions, the density of arthropods increased on average by 37% when the vertebrate predators were removed (Figure 1, Table S6). While the effect of vertebrates on arthropods was significant even when combined with the effect of ants (33% increase, Figure 1, Table S6), the exclusion of ants alone had no significant effect on arthropod density, which only increased by 12% based on the model predictions (Figure 1, Table S6).

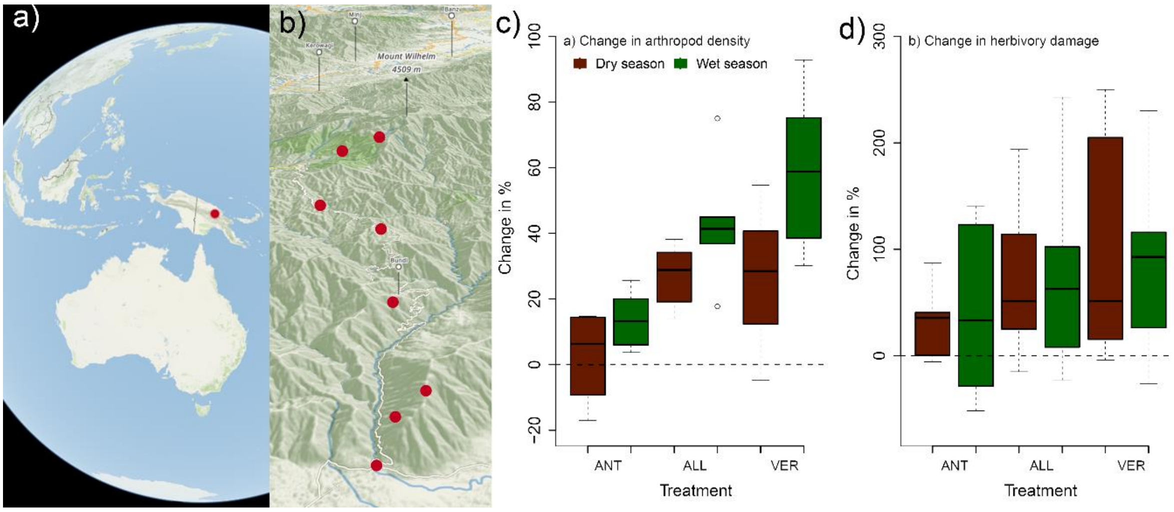
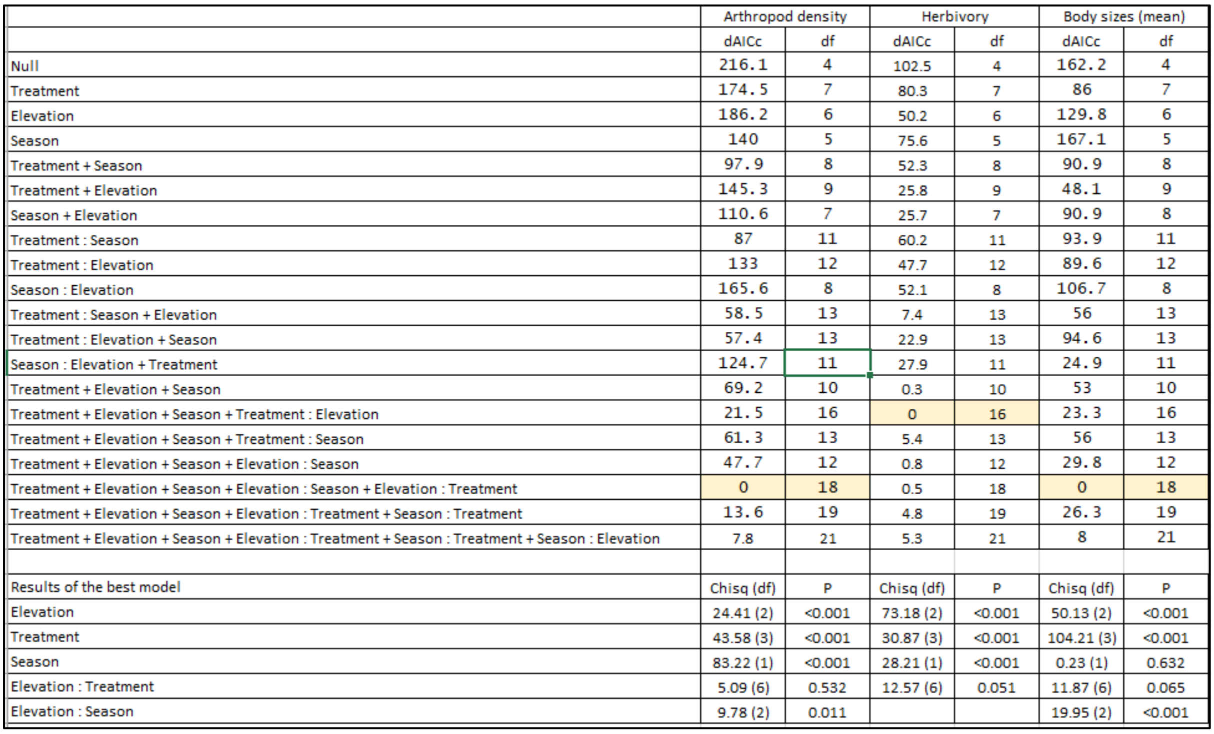


Figure 1. Location of Papua New Guinea and Mt. Wilhelm range (red dot) in Southwest Pacific (a) and illustrative locations of the 8 study sites along the range (b). Both maps were produced by Mapy.cz under the licence Creative Commons 4.0 (CC-BY-SA 4.0). The overall changes in the arthropod densities (c) and herbivory damage (d) in wet and dry season (marked by colour) after the predators were excluded, irrespective to elevation. Zero change (marked by a dashed line) means that the arthropod density or herbivory damage did not change from the respective control treatment. Values below 0 mean that the respective value was higher at control tree than in predator exclusion treatment. Treatments: ANT = saplings from which ants are excluded by tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded. Boxplots are showing medians, 25 and 75% quartile, maxima, and minima. Outliers are marked by empty circle. One outlier (value 550) is not shown for VER treatment in dry season to make the graph more readable. Figure 1. is based on the actual change in densities and herbivory, while Figure S3 shows changes predicted by the best models, see also Table S6 and S7 for details.

Elevation and the interaction between elevation and treatment, and elevation and season, also had significant effects on the resulting density of arthropods (Figure 2, Table 1).

Table 1. Corrected Akaike Information Criterion (AICc) of regression models examining abundances of all arthropods, herbivory damage, and mean body size of arthropods observed on saplings in the wet and dry season (season) and excluding various predators (treatment) 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 density		Herbivory		Body sizes (mean)	
	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

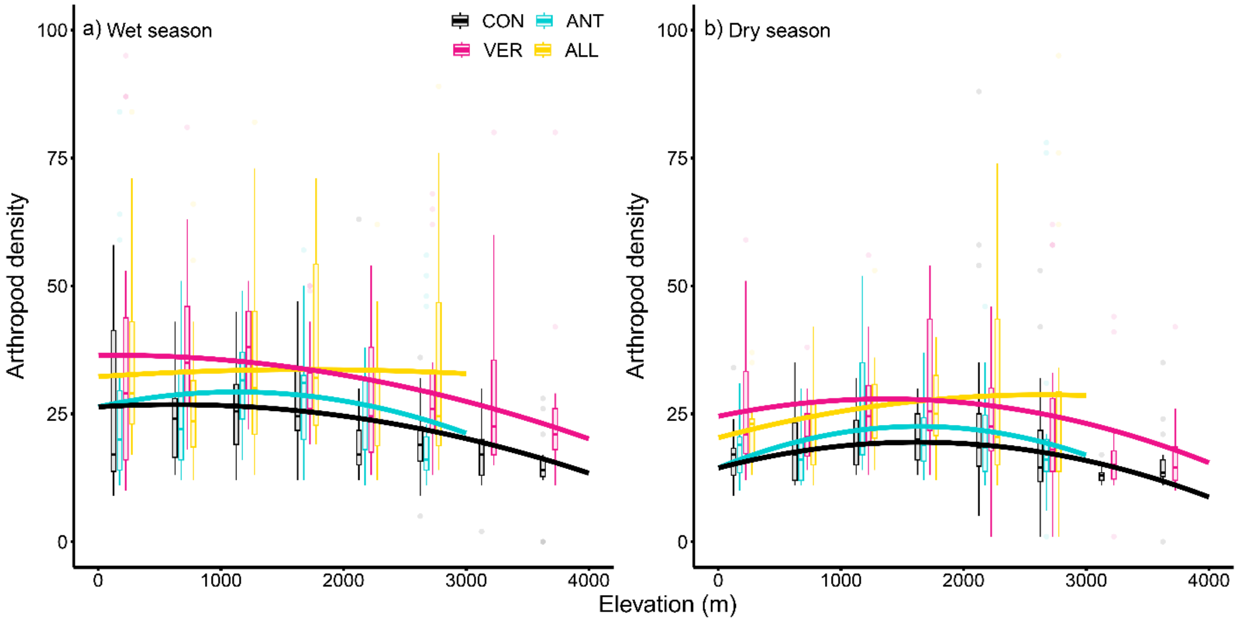


Figure 2. Effect of the predator exclusion (treatment) on the densities of all arthropods on saplings along the elevational gradient of Mt Wilhelm in the wet (a) and dry season (b). The curves show predicted values from the linear model which includes season, elevation, and treatment, using the interaction 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 tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded. Boxplots are showing medians, 25 and 75% quartile, maxima, and minima. Significance of the differences between treatments are in Table S6.

Change in herbivory

Predator exclusion, elevation and season had a significant additive effect on leaf area loss (Figure 3, 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, the 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), according to the models. 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 1, 3). The increase in leaf damage seemed to be highest in the lowest and upper most elevations (Figure 3, Table S7).

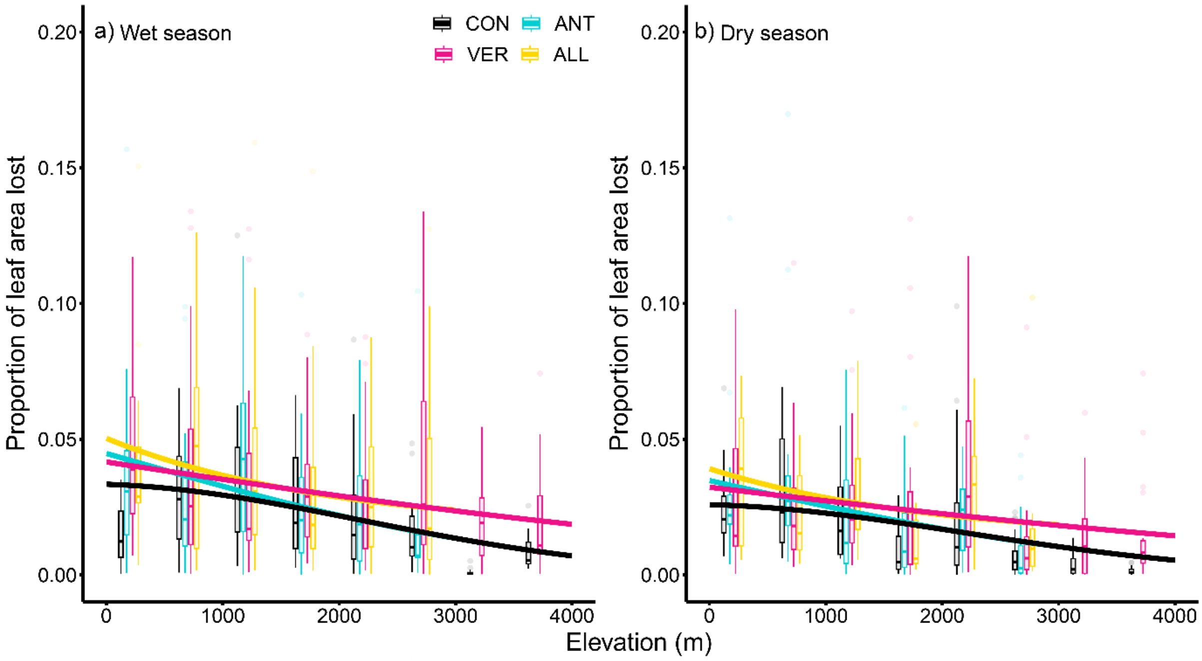


Figure 3. Effect of the predator exclusion (treatment) on leaf damage (m^2 per sapling) on saplings along the elevational gradient of Mt Wilhelm in the wet (a) and dry season (b). The curves show predicted values from the glmmTMB models which include season, elevation and treatment as fixed factors and 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 tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded. Boxplots are showing medians, 25 and 75% quartile, maxima, and minima. Significance of the differences between treatments are in 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 4, Table 1). While model selection identified season as a significant factor due to its importance in model interactions, the effect of season alone was not significant (Table 1). This means that the seasonal effect cannot be described properly because of its variation across elevations. Very similar results, yet including the effect of seasonality more strongly, were found when we considered the body size of all individual arthropods instead of the mean per sapling (Table S8, Figure S4). The arthropods in caged treatments were significantly bigger than arthropods collected from control saplings and saplings from which ants were excluded (Figure 4, Table 1). The majority of arthropods collected during the experiment were very small, with larger arthropods (i.e., greater than ca. 2.2 cm in length) found exclusively in the caged treatments (VER and ALL) to which vertebrate predators had no access.

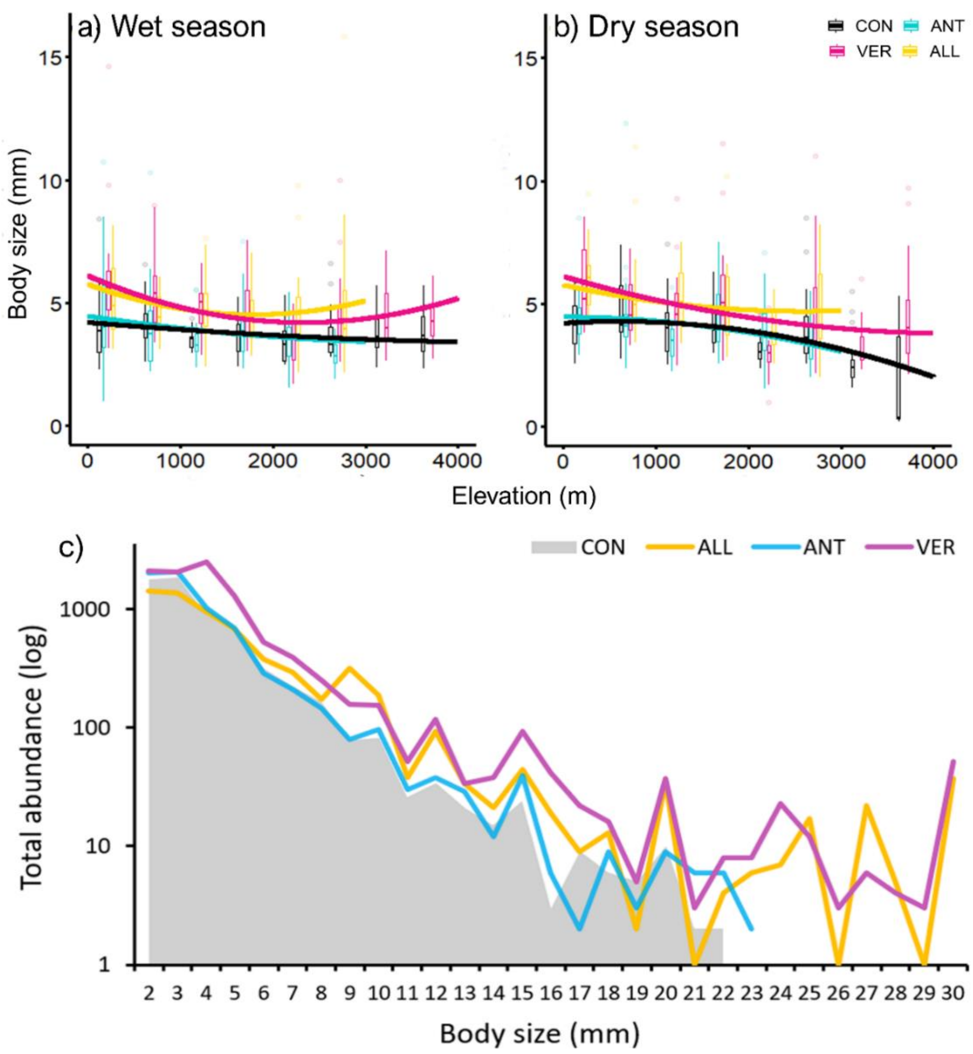


Figure 4. Effect of the predator exclusion on mean body size of the arthropods collected from saplings along the elevational gradient of Mt Wilhelm in the wet (a) and dry season (b). The curves show predicted values from the linear model which included season, elevation, and treatment as a fixed factor. See Table S6 for model results. The occurrence (log of the total density) of arthropods of a given body size in each of the four treatments is shown in (c). Treatments: CON = control saplings with free access of predators, ANT = saplings from which ants are excluded by tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded. Boxplots (a, b) are showing medians, 25 and 75% quartile, maxima, and minima.

Changes in community composition

Overall, 12,177 arthropod individuals were identified as predatory arthropods (i.e., 46% of all arthropods), while only 4,085 (i.e., 16%) were herbivores potentially responsible for leaf damage and 10,065 (i.e., 38%) were arthropods which had no relationship to chewing herbivory (Table S3). The majority of predatory arthropods (8,221, i.e., 68% of all predatory arthropods) were spiders. Absolute densities as well as relative densities 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 5). Across the whole study, Araneae, Diptera, Hemiptera, and Lepidoptera larvae increased their densities 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 vertebrate predators were excluded (Figure 5).

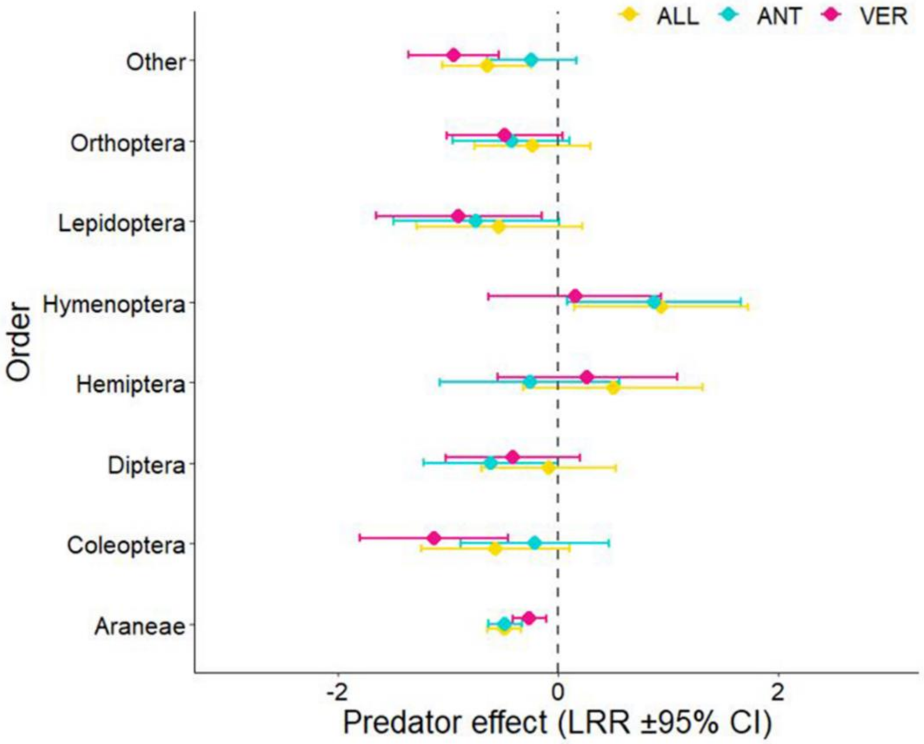


Figure 5. Caterpillar graph showing how individual orders of arthropods responded to the predator exclosure treatments. The X-axis shows mean effect sizes of natural log ratios (LRR

= 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 the control (presence of predators), as the density of arthropods in exclosures increased and caused potentially higher herbivory damage to plants. Treatments: ANT = saplings from which ants are excluded by tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded.

Predator communities and their relation to the observed cascading 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 densities of prey (Figure 6), but not with the effect measured on herbivory damage (Figure S3). Abundances of insectivorous birds, and thus those potentially responsible for attacks, peaked at mid-elevations (1700 - 2700 m) and correlated positively and significantly (given the low power of the analysis and strong effect size) with the effect of vertebrate exclosure treatment on arthropod densities ($R = 0.71$, $P = 0.049$, Figure 6a). 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 6b). 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 at least partly responsible for 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 densities of prey, and abundance of these insectivorous 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 abundances decreased with elevation. Despite the positive relationship, neither the number of trees with ants on them (R = 0.25, P = 0.56) nor the abundance of the ants (R = 0.14, P = 0.74, Figure 6c) correlated significantly with the effect of the ant exclosures on densities of arthropods.

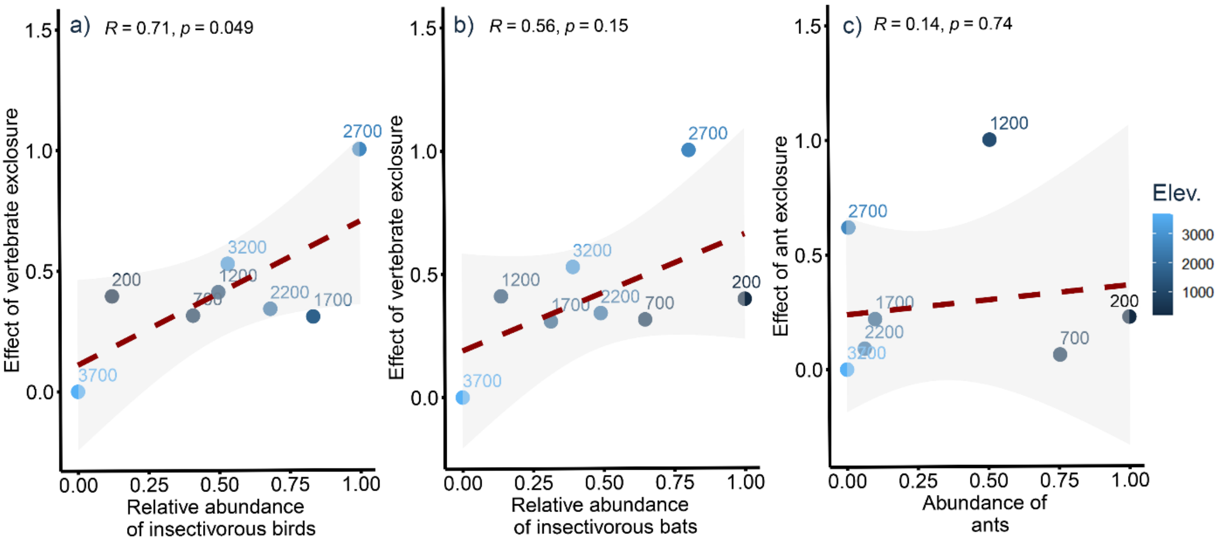


Figure 6. Correlations between the effect of vertebrate exclosures (a, b) and ant (c) exclosures on densities of arthropods (LRR calculated from raw data and normalized data) and relative abundances (normalized) of insectivorous birds (a), insectivorous bats (b) and abundances of ants (c) potentially feeding on the experimental saplings. Shades of blue represent elevations.

Discussion

Predator removal increases arthropod densities on plants, which is in line with our first hypothesis (*H1*). It is important to note that the increased numbers of arthropods may be caused by both a lack of predation and a lack of movement. This can result in higher prey numbers due to improved survival rates as well as increased performance and willingness to stay in the area. Overall, arthropod densities increased by ca. 37% after the removal of flying insectivorous vertebrates, which is matching the estimates from two global reviews reporting an increase by ca. 39% (Mooney, et al. 2010) and 69 % (Sam, et al., 2022). The result of 12% density increase after ant removal is in line with what was found globally in a meta-analysis by Sam et al (2022), while it contrasts with results by Rosumek et al 2009, who found 70% increase in arthropod abundance when ants were excluded. However, Rosumek's et al. (2009) study analyses datasets comprising 70% 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. It is important to note that the treatment itself almost completely removed ants from our experimental saplings, and ants represented ca. 2% of all arthropods in samples from our controls, thus impacting the effect of the treatment on the total density of the arthropods.

Contrary to our expectations for the highest effect of predator exclusion between 700 and 1700 m a.s.l. (*H1B*), the effect of insectivorous vertebrates on arthropod density increased both towards the lowest (200 and 700m) and the highest elevations (above 2700m), and was higher during wet than during dry season. It is important to remember, that both groups of flying vertebrate predators (birds and bats) were excluded in the current study. While the relative abundance of insectivorous bats was high at low elevations and at 2700 m a.s.l., the abundance of insectivorous birds peaked at the mid-elevations (1700 and 2200 m a.s.l.). Moreover, most of the gleaning bats are found in the lowlands. We can only speculate that bats are responsible, at least partly, for the predation at low elevations as our data are not suited to detect subtle elevational trends. Despite having just eight points in the correlation limits the robustness of the analyses, we showed that predation risk on arthropods was correlated with the abundance of predatory birds (and less so for 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 indicate that the abundances of birds are a better correlate for the effect of predators than their richness or biomass. Observations made during our long-term surveys, and in an earlier study, indicate that most breeding of insectivores occurs at the onset of rains, when the arthropods become more abundant in response to leaf flushing (Bell, 1982, Sam, et al. 2015, Sam, et al. 2017), which can lead to strong effects of predator exclosures during wet season, as observed.

Our current results further imply different trends appearing to emerge from studies of predation with different methodologies. We argue 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 densities of arthropods and their predators. Dummy prey predation rate by birds along the same gradient peaked at lower mid-elevations (Sam, et al. 2015), where the abundances of insectivorous birds peaked, therefore we expected that the highest effect of predator exclusion between 700 and 1700 m a.s.l.. However, we did not observe this trend in more natural, exclosure experiments, where natural densities of predators play their role.

Predator exclusion has 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 even though the mesh size (3x3 cm) of the cages was likely also preventing access to large arthropods. Arthropod mean body size increased primarily at low elevations where many large arthropods occur (Sam, et al. 2017, Horne, et al. 2018), but also at the highest elevations. In contrast to vertebrate insectivores, the exclusion of ants did not have any effect on the mean body size of arthropod communities. As such this contradicts the 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 hunt collectively for large arthropods (Schmidt and Dejean 2018). This might lead to a balanced consumption of arthropods of all sizes.

Overall, the absence of predators allowed various, but not all, groups of arthropods to increase their densities (*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 the control and vertebrate-protected saplings. Diet analyses of birds from the same gradient also showed that ants are not important prey for birds (Sam, et al. 2017). Other studies concur with this, where 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) were found to be preferred prey of birds, but not ants (*H4*). This seems to be reflected in our current results, as these groups of arthropods increased their densities significantly after the insectivore 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 densities significantly, but spiders seemed to be the most affected. This is in line with the results of earlier studies which showed that spiders increased their densities by more than 100% (Rosumek, et al. 2009) and by 84% (Sam, et al. 2022) in the 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 as spider density was higher in the absence of ants than in the absence of vertebrates. Results of existing studies are vague, and despite most of the studies typically showing ants to feed on eggs and insect larvae primarily (Gathalkar and Sen 2018), there is some evidence of them hunting spiders also (Risch and Carroll 1982).

The standing herbivory on control saplings along Mt Wilhelm was 5 to 10 times lower than the global estimates of herbivory for tropical forests (10-40%, Coley and Barone 1996), yet comparable to analogous studies relying on precise measures of herbivory in blind experiments (Sam, et al. 2020, Kozlov et al. 2014, Zava & Cianciaruso 2014). The change in herbivory following the removal of predators was also surprising (*H5*). Herbivory damage increased significantly both after the removal of ants and vertebrate predators, but the effect varied in time and space. Herbivory across the whole gradient in the wet season increased on average by 84, 76 and 41% after the removal of all predators, vertebrate predators, and ants respectively. The pattern was similar, despite being lower in the dry season. All increases are higher than the previous global estimates which predicted increases in leaf herbivory of ca. 40 - 47% in the absence of vertebrate predators (Mooney, et al. 2010, Sam, et al., 2022). The effect of ants on herbivory at low elevations was actually stronger than their effect on the density of herbivore arthropods, where ants increased herbivory by ca. 130% and herbivorous arthropods only by 3%. Similarly, Rosumek et al. (2009) showed that ant removal increased herbivory by more than 95%, whereas the density of herbivorous arthropods increased by ca. 60% in the tropics.

The overall effect of predators on lower trophic levels was affected by season (*H1A*). The removal of vertebrate predators in the wet season led to increases in herbivory of ca. 100-230%. In the wet season, the effect was highest at the lowest and highest elevations. In contrast, in the dry season, the increases in herbivory were generally lower than in the wet season but an extreme increase of 555% was detected at 3700 m a.s.l.. The seasonal differences are likely to be much higher in more seasonal habitats than those of the northern side of Papua New Guinea, which is known to be only weakly seasonal (Novotny and Basset 1998, Wright, et al. 1997). From the global perspective, our results indicate that changes in rainfall regime will affect trophic cascades significantly but site-specifically. The increases of herbivory damage in the absence of predators were especially high in the most productive lowland sites during the wet season. Considering the elevational gradient as a proxy of the productivity gradient (with the wettest and warmest sites in lowlands), we can expect an increase in herbivory damage with globally increasing temperature but a decrease in herbivory if precipitation patterns get disturbed. If we wish to better understand elevational trends in herbivory and plant defences, then it is necessary to perform analyses based on multiple traits of direct and indirect defences and to link these to datasets on arthropods herbivores.

In conclusion, we show that flying insectivorous vertebrates suppress arthropods effectively, yet their impact differs among various groups of arthropods. The predation pressure of vertebrate insectivores is robust across the whole elevational gradient and translates to significantly higher plant herbivory in the absence of predators. Despite our results being idiosyncratic of where the experiment is conducted, and we would need multiple mountains with predators excluded in a similar way to know the true contribution of vertebrates versus ants, our results show that the relative contribution of birds and bats differs along the elevational gradient of Mt. Wilhelm on tropical island Papua New Guinea. In contrast, ants did not suppress arthropods and herbivory damage significantly. The site at 200 m, where the abundances of ants are the highest, was the only site where the effect of ants translated into significantly increased herbivory. Similarly, there might be biomes that rely more on ants than on vertebrate predators, as not all tropics are equal. For example, predator exclosures on mainland tropical mountains that have some of the highest diversity of ants could come with radically different conclusions. Insectivorous vertebrates, but not ants, had a stronger negative effect on large arthropods which can further negatively impact herbivory rates. While some general patterns have emerged, we recommend that future experiments consider factors such as intraguild predation, mesopredators, and plant defences, and that these experiments include detailed predator surveys. These factors can significantly influence the strength of trophic cascades.

Data availability statement

All data and scripts are available at GitHub https://github.com/KatkaSam/GRAD_Exclosures (public).

Bioscatch

Katerina Sam is a head of Laboratory of Multitrophic interactions and the Department of Ecology at the Entomology Institute, where she studies relationships between insectivorous predators, insect and plants. This work represents her earlier postdoctoral experiment, which further grew into a European Research Council funded project. She and her colleagues study various aspects of ecology and biodiversity of Mt. Wilhelm from 2008.

Author contributions

KS conceived the ideas, secured funding and conducted the experiment with help of BK, PA and ES conducted the survey of insectivorous predators, LRJ assisted with statistical analyses to KS. All authors contributed to writing and edited the first draft written by KS.

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Supporting information

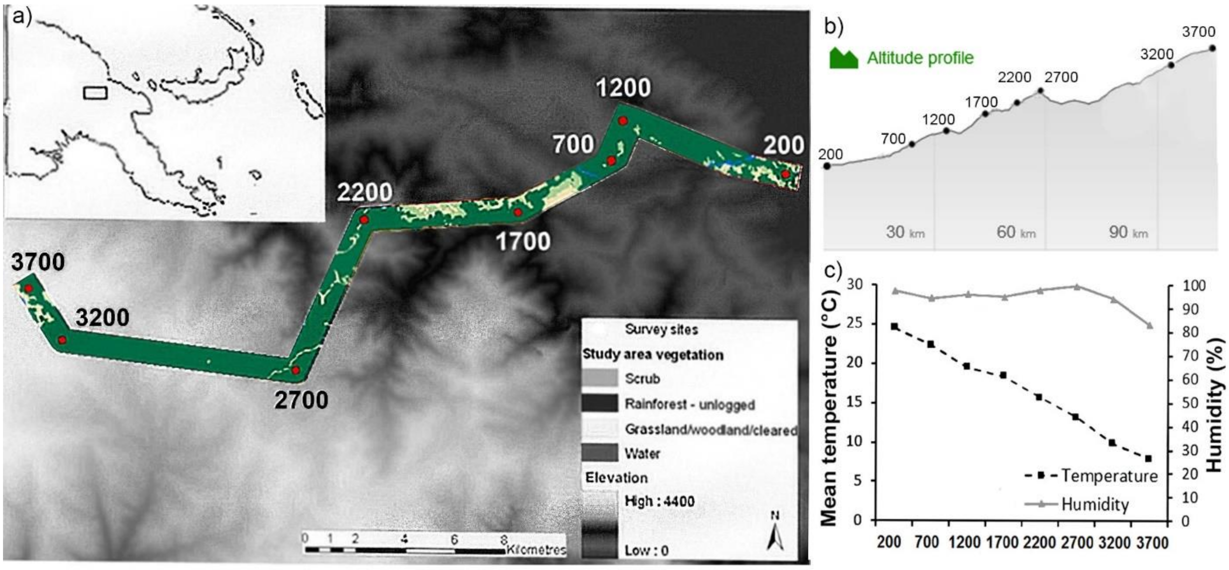

Figure S1. Outline map of Papua New Guinea, with the location of the Mt. Wilhelm elevational gradient indicated by square (insert). Map of the Mt. Wilhelm elevational gradient showing all eight elevational study sites. Insert shows location of the elevational range within Papua New Guinea. Darker colours are marking lower elevations and lighter colours mark higher elevations. Note that data from six lower elevational study sites were analysed separately from the full elevational gradient due to different plant species composition (a). Elevational profile of the Mt. Wilhelm transect following the available track/road, with the eight elevational study sites marked (b). Mean daily temperature and humidity at each of the study sites (c).

Table S1. Plant species, treatments, and the number of samples (total = 1,115) collected from each treatment from them at each elevational study site. ALL = vertebrate predators and ants excluded, ANT = ants excluded, VER = vertebrates excluded, CON = control saplings without exclusion.

Plant species	Treatment	200	700	1200	1700	2200	2700	3200	3700
Ficus arfakensis	ALL	8	4		14				
	ANT	8	6		12				
	CON	8	4		12				
	VER	10	6		18				
Ficus badiopurpurea	ALL		8		6				
	ANT		8		4				
	CON		4		8				
	VER		7		2				
Ficus congesta	ALL	6							
	ANT	12							
	CON	10							
	VER	12							
Ficus conocephalifolia	ALL	8	4						
	ANT	4	4						
	CON	4	8						
	VER	4	4						
Ficus endochaete	ALL			24		8	6		
	ANT			28		2	4		
	CON			36		2	4		
	VER			28		6	8		
*Ficus hahliana**	ALL	12	3	2		2	12		
	ANT	8	10	6		6	12		
	CON	14	6	2		4	12		
	VER	8	2	2		6	6		
Ficus hispidioides	ALL	4							
	ANT	8							
	CON	4							
	VER	6							
Ficus hombroniana‡	ALL		4		4	10			
	ANT		4		2	12			
	CON		2		8	4			
	VER		2		4	4			
Ficus iodotricha	ALL				4	4	4		
	ANT				10	2	9		
	CON				4	6	2		
	VER				6	12	6		
Ficus mollior	ALL				6				
	ANT				4				
	CON				6				
	VER				2				
Ficus saccata	ALL					6	18		
	ANT					2	14		
	CON					11	21		
	VER					8	20		
Ficus subcuneata	ALL		14						
	ANT		2						
	CON		8						
	VER		12						
Ficus trichocerasa•	ALL		2	14	6				
	ANT		6	7	7				
	CON		8	2	2				
	VER		6	10	8				
Ficus wassa#	ALL					10			
	ANT					16			
	CON					14			
	VER					4			
Pittosporum berberidoides	CON							10	16
	VER							10	16
Myrsine womersleyi	CON								12
	VER								10
Myrsine papuana	CON							18	6
	VER							10	10
Macaranga melanosticta	CON							12	6

Notes to Table S1: *F. hahliana* is confirmed as a good species from 200-1200m of our elevational gradient. After this (1700m-2700m) a close relative/sister species occurs. However, this potential split was discussed only recently based on molecular differences (Segar et al. 2016). We were not able to distinguish the two species in the time of our experiment. ǂ *F. hombroniana* is found between 200-1200m. There are a few individuals at 1,700m but most individuals classified as *F. hombroniana* here are probably (and at 2200m) the closely related *F. ihuensis.* • *F. trichocerasa* has two sub-species along the elevational gradient. *F. trichocerasa* subsp. *trichocerasa* occurs between 200-1700m and *F. trichocerasa* subsp. *pleioclada* occurs between 1700m and 2200m. They co-occur at 1700m, and both subspecies were included in our study as they are difficult to distinguish in the field at 1700m. # *F. wassa* comprises several varieties along the elevational gradient of Mt. Wilhelm (Berg and Corner 2005). The varieties included in our study were *F. wassa* var. nubigena which occurs along the gradient from 1300 to 3000 m and *F. wassa* var. wassa which occurs along the whole gradient.

Table S2. Number of saplings set for the treatments at individual elevational study sites; the first day when the treatments were set (T_0), when the effect was surveyed for the first time and second time (S1, S2). We selected total of 560 saplings for the experiment, not all sapling however survived until the end of the experiment which leads to discrepancies between Table S2 and Table S1 (1,115 samples collected instead of 1,120 predicted). Treatments: CON – control trees ANT - only ants excluded, VER – only vertebrates excluded, ALL – vertebrates and ants excluded. Setting and survey of the exclosures usually took 2-4 days and was conducted by two teams working simultaneously or together according to safety, terrain, and safety needs.

Elevation	CON	ANT	VER	VER+ANT
200	20	20	20	20
	T_0:1May14 S1:1Nov14 S2:15Apr15			
700	20	20	20	20
	T_0:29Apr14 S1:27Oct14 S2:7Apr15			
1200	20	20	20	20
	T_0:25Apr14 S1:21Oct14 S2:30Mar15			
1700	20	20	20	20
	T_0:27Apr14 S1:25Oct14 S2:8May15			
2200	20	20	20	20
	T_0:14Apr14 S1:6Oct14 S2:16Mar15			
2700	20	20	20	20
	T_0:11Apr14 S1:8Oct14 S2:19Mar15			
3200	20	NA	20	NA
	T_0: 4Apr14 S1:31Aug14 S2: 16Feb15			
3700	20	NA	20	NA
	T_0: 2Apr14 S1:31Aug14 S2:9Feb15			

Table S3. List of the insect groups identified within each feeding guild, their abundances on individual treatments in wet and dry season. Predators = arthropods able to kill other arthropods.

	Wet				Dry			
	ALL	ANT	CN1	VER	ALL	ANT	CN1	VER
Predators	1802	1957	1923	2597	1137	1173	972	1301
Araneae	1355	1304	1013	1253	884	942	601	869
Chilopoda	10	3	2	8	19	4	9	11
Coleoptera	283	488	466	545	200	187	154	177
Anthribidae	*3*	*2*				*1*		
Cantharidae	*9*	*53*	*74*	*69*	*17*	*15*	*19*	*8*
Carabidae	*5*	*5*	*2*	*25*	*25*	*6*	*8*	*19*
Cleroidea						*2*		
Malachiidae					*14*	*25*	*23*	*22*
Pselaphidae	*4*	*2*			*1*	*4*	*1*	*1*
Staphylinidae	*262*	*426*	*390*	*451*	*143*	*134*	*103*	*127*
Hemiptera	4			3				
Gelastocoridae	*2*			*1*				
Nabidae	*2*			*2*				
Hymenoptera	143	156	427	776	30	37	201	231
Ant	*15**	*37**	*342*	*670*	*9**	*23**	*196*	*214*
Wasp	*128*	*119*	*85*	*106*	*21*	*14*	*5*	*17*
Mantodea		2	5	3		1	2	2
Neuroptera	2	1	1	4				4
Mantispidae	*2*	*1*	*1*	*4*				*4*
Opiliones	5	3	9	4	3	1	5	5
Scorpiones				1	1	1		2
Herbivory - chewers	694	951	796	1213	425	411	409	474
Coleoptera	350	625	527	625	186	215	219	198
Chrysomelidae	*151*	*336*	*242*	*280*	*96*	*83*	*68*	*50*
Coccinellidae	*22*	*16*	*12*	*19*	*5*	*1*		*2*
Coleoptera_Larvae	*26*	*23*	*32*	*30*	*3*	*14*	*1*	*12*
Curculionidae	*127*	*235*	*234*	*275*	*80*	*116*	*150*	*133*
Meloidae	*4*	*5*	*5*	*2*	*0*	*0*	*0*	*1*
Scarabeidae	*20*	*10*	*2*	*19*	*2*	*1*	*0*	*0*
Gastropoda	19	15	7	37	16	17	16	26
Lepidoptera_Larvae	150	166	108	329	74	43	67	83
Orthoptera	165	142	151	216	144	128	99	162
Caelifera	*45*	*29*	*40*	*68*	*85*	*74*	*62*	*84*
Ensifera	*120*	*113*	*111*	*148*	*57*	*54*	*37*	*78*
Phasmatodea	10	3	3	6	5	8	8	5
Unknown relationship	19	28	12	20	144	198	178	187
Other Coleoptera	68	67	84	85	79	73	78	103
Other Hemiptera		16	1	7	14	53	52	39
Other Hymenoptera	19	12	11	13	49	69	45	44
Other Neuroptera		2			2	3	3	1
No relationship	1188	1630	1349	3268	710	480	573	878
Acarina	1		1	2	3		3	43
Pseudoscorpiones		1					1	2
Amphipoda		11	5	5		4		
Anellida		19		13	6	1		6
Apterygota					2			5
Blattodea	164	36	27	200	95	15	19	82
Coleoptera	37	42	49	69	41	47	59	42
Anobiidae		*4*	*2*	*3*				
Cerambycidae	*24*	*11*	*13*	*26*	*16*	*7*	*6*	*11*
Dermestidae						*1*		
Elateridae	*9*	*27*	*30*	*39*	*6*	*10*	*20*	*13*
Erotylidae					*1*			*1*
Eucnemidae						*3*	*1*	
Leiodidae						*1*	*15*	*3*
Lucanidae								*1*
Lycidae	*1*		*4*	*1*	*4*	*18*	*4*	*2*
Mordellidae					*2*	*1*	*2*	*2*
Nitidulidae					*3*	*3*	*10*	*1*
Oedemeridae							*1*	*1*
Phalacridae	*2*							
Tenebrionidae	*1*				*9*	*3*		*7*
Collembola	106	108	126	220	53	42	53	101
Crustacea					8	10	13	6
Dermaptera	16	14	12	25	24	12	23	31
Dictyoptera	1							
Diplopoda	35	9	35	49	52	40	20	55
Diptera	183	181	227	391	157	173	229	236
Embioptera		2						

	Wet				Dry			
	ALL	ANT	CN1	VER	ALL	ANT	CN1	VER
No relationship (cont.)	1188	1630	1349	3268	710	480	573	878
Hemiptera	355	547	625	580	143	75	83	110
Aleyrodidae	*1*	*2*	*1*	*3*		*1*		
Alydidae	*11*	*26*	*26*	*53*	*6*	*4*	*2*	*2*
Aphididae	*35*	*154*	*203*	*39*	*11*	*7*	*6*	*2*
Aradidae				*1*				
Asopinae	*2*			*2*				
Auchenorrhyncha					*10*	*8*	*16*	*15*
Berytidae			*2*					
Cercopoidea	*2*	*13*	*1*	*5*		*8*		
Cicadellidae					*1*			*1*
Cicadellidae_Larvae					*1*	*3*	*2*	*13*
Fulgoromorpha				*2*	*11*		*1*	*16*
Iassidae						*1*	*2*	
Cicadelidae	*95*	*163*	*196*	*177*	*29*	*8*	*14*	*16*
Cicadelidae_Larvae	*14*	*8*	*4*	*17*	*1*			
Lygaeoidea	*1*	*1*		*6*			*3*	
Meenoplidae								
Membracidae			*1*			*1*	*1*	*4*
Membracidoidea					*3*	*2*	*2*	*1*
Miroidea							*1*	
Miridae	*61*	*92*	*83*	*142*	*26*	*12*	*2*	*7*
Miroidea					*6*	*13*	*22*	*9*
Pentatomidae	*16*	*17*	*12*	*29*	*4*	*6*	*6*	*10*
Fulgoromorpha	*36*	*37*	*41*	*49*	*2*	*1*	*1*	*2*
Fulgoromorpha_Larvae	*31*		*3*	*3*				*1*
Psylloidea					*1*		*2*	*1*
Psylloidea					*25*			*3*
Pyrrhocoridae	*12*	*5*	*7*	*6*	*2*			*1*
Reduviidae	*21*	*20*	*18*	*34*	*2*			*3*
Rhopalidae	*6*	*3*	*15*					
Rhyparochromidae	*1*							
Scutelleridae	*10*	*3*	*5*	*7*	*1*			
Sternorrhyncha					*1*			
Tessaratomidae	*1*	*3*	*7*	*2*				
Tessaratomidae_Larvae		*2*						
Tingidae				*3*				*1*
Heteroptera					*8*	*1*		
Hirudinea	2		3					
Hymenoptera	1		6	1			1	
Apoidea	*1*		*6*	*1*			*1*	
Isopoda	23	7	24	30	13	3	15	16
Lepidoptera	40	28	26	46	20	9	19	19
Nematoda	2			2		1		2
Neuroptera	9	2	5	8	6		1	9
Chrysopidae	*7*	*2*	*5*	*6*	*4*		*1*	*4*
Neuroptera								*3*
Sisyridae	*2*			*2*	*2*			*2*
Odonata					1	1		1
Orthoptera_Larvae					1			1
Other stages	24	17	14	27	36	19	18	75
Egg_Larvae		*4*	*8*	*5*	*1*	*1*		*29*
Larvae_Larvae	*19*	*9*	*4*	*11*	*35*	*18*	*18*	*45*
Pupae_Larvae	*5*	*4*	*2*	*11*				*1*
Plecoptera		5	5	1		3		1
Psocoptera	168	203	138	237	30	15	9	26
Thysanoptera	18	395	14	1358	4	5	5	5
Thysanura	3	3	4	2				1
Trichoptera			3	2	7	4	2	3

Additional methods – survey of predators

Bird survey

Bird communities here have been repeatedly surveyed by point counts as part of long-term monitoring efforts, with this methodology and data published in several studies (Marki, et al. 2016, Sam and Koane 2014, Sam, et al. 2019). In short, 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.

Here 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, i.e., 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). Our analyses here 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 included the earlier data from 2013 to calculate mean abundances of insectivorous birds more robustly, as a 3-day long survey alone might not be sufficiently describing these tropical bird communities. 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). We also extracted the body mass of each species and used this to calculate total bird biomass 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). This method and data were published in Sivault, et al. (2022). In short, 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, in line with the bird transect methods 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. We distinguished individual echolocation call types within the recordings and later identified these 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 as indicated by (Kerbiriou, et al. 2019). Finally, we calculated biomass of bats at each elevation using the average maximum body mass of males and females of each bat species found in the literature (Bonaccorso 1998, Flannery 1995). Any missing body mass information was supplemented with the body mass of the closest species(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 also by the tuna bait method in May-June 2014. Baits were filled with commercial canned tuna in oil, which is a standard method in studies of foraging ant communities. One teaspoon of tuna was placed as a bait under a strip of gauze at breast height on each of the saplings. Baits were inspected three hours following their exposure. The abundance of ants was counted on each bait. 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). We correlated ant abundance data collected by tuna baits from understory saplings and hand collected data from the trunks. The same survey was conducted at 3200 and 3700 m above sea level and detected no ants, which is in line with results from previous studies of ant communities along the same gradient (Colwell, et al. 2016, Moses, et al. 2021, Sam, et al. 2015).

Table S4. List of recorded bird species, their feeding specialization, occurrence in forest strata (in %), body weight and abundance at each of the surveyed study sites.

HBW_Name	HBW_ScientificName	GuildDetail	Guild	Ground	Low	Middle	Canopy	Mass	200	700	1200	1700	2200	2700	3200	3700
White-eared Catbird	*Ailuroedus buccoides*	FRIN	FR	0	50	50	0	138.00	8	1	1					
Black-eared Catbird	*Ailuroedus melanotis*	FRIN	FR	50	0	0	50	228.00					1			
Papuan King-Parrot	*Alisterus chloropterus*	FRSE	FR	0	0	50	50	161.33		2			2	5		
MacGregor's Bowerbird	*Amblyornis macgregoriae*	FRIN	FR	0	0	0	100	126.00				2	1	2		
Singing Starling	*Aplonis cantoroides*	FRIN	FR	0	0	0	100	58.33	21							
Stephanie's Astrapia	*Astrapia stephaniae*	FRIN	FR	0	0	50	50	137.50					1	6	50	6
Sulphur-crested Cockatoo	*Cacatua galerita*	SEFR	FR	25	25	25	25	894.00	48	43	2	3				
Pacific Emerald dove	*Chalcophaps longirostris*	FRGR	FR	0	0	0	100	166.00	5							
Stephan's Dove	*Chalcophaps stephani*	SEFR	FR	100	0	0	0	122.00	8	2	7					
Josephine's Lorikeet	*Charmosyna josefinae*	FRIN	FR	0	0	50	50	36.00					1			
Magnificent Bird-of-paradise	*Cicinnurus magnificus*	FRIN	FR	0	50	50	0	90.50		16	29	1				
King Bird-of-Paradise	*Cicinnurus regius*	FRIN	FR	0	0	0	100	51.00	11	1						
Loria's Satinbird	*Cnemophilus loriae*	FR	FR	0	50	50	0	88.00				3	1		2	
Crested Satinbird	*Cnemophilus macgregorii*	FR	FR	0	50	50	0	92.50					2	5	18	
Metallic Pigeon	*Columba vitiensis*	FRVG	FR	25	25	25	25	388.50						3		
Gray Crow	*Corvus tristis*	FRIN	FR	50	0	0	50	635.00	17	14						
Double-eyed Fig Parrot	*Cyclopsitta diophthalma*	SEFR	FR	0	0	0	100	40.50	6	7	17	9				
Orange-breasted Fig Parrot	*Cyclopsitta gulielmitertii*	SEFR	FR	0	0	0	100	31.33	9							
Rufescent Imperial-Pigeon	*Ducula chalconota*	FR	FR	0	0	50	50	613.00				1	1	1		
Pinon's Imperial-Pigeon	*Ducula pinon*	FR	FR	0	0	0	100	792.50	4	7	10					
Zoe's Imperial-Pigeon	*Ducula zoeae*	FR	FR	50	0	0	50	585.67	16	24	23					
Eclectus Parrot	*Eclectus roratus*	FRSE	FR	0	0	0	100	466.00	22	22						
Black-bellied Cicadabird	*Edolisoma montanum*	FRIN	FR	0	33	33	33	63.87		2	2	40	1	2		
Black Sicklebill	*Epimachus fastosus*	FRIN	FR	0	0	50	50	215.75				1	3	5		
Pacific Koel	*Eudynamys orientalis*	FRIN	FR	0	0	0	100	256.50	8	6						
Cinnamon Ground Dove	*Gallicolumba rufigula*	FRGR	FR	100	0	0	0	129.00	2		5					
Red-cheeked Parrot	*Geoffroyus geoffroyi*	SEFR	FR	0	0	0	100	152.67	15							
Papuan Mountain-Pigeon	*Gymnophaps albertisii*	FR	FR	0	0	0	100	259.00	5	4		32	53	53		4
New Guinea Bronzewing	*Henicophaps albifrons*	FRIN	FR	25	25	25	25	247.00		2						
Yellow-breasted Satinbird	*Loboparadisea sericea*	FR	FR	0	33	33	33	64.75						1		
Greater Lophorina	*Lophorina superba*	FRIN	FR	0	33	33	33	82.25				24				
Amboyna Cuckoo-Dove	*Macropygia amboinensis*	FRSE	FR	25	25	25	25	125.00	9	4	38	3	2			
Black-billed Cuckoo-Dove	*Macropygia nigrirostris*	FRSE	FR	25	25	25	25	78.05		2		20	36	8		
Spotted Berrypecker	*Melanocharis crassirostris*	FRIN	FR	0	33	33	33	18.00				4				
Mid-mountain Berrypecker	*Melanocharis longicauda*	FRIN	FR	25	25	25	25	14.00				1		1		
Black Berrypecker	*Melanocharis nigra*	FRIN	FR	0	50	0	50	14.00	21	36	66	6	2			
Streaked Berrypecker	*Melanocharis striativentris*	FR	FR	0	0	100	0	18.55				4		2		
Fan-tailed Berrypecker	*Melanocharis versteri*	FRIN	FR	0	33	33	33	14.85				24	38	32	22	2
Smoky Honeyeater	*Melipotes fumigatus*	FRIN	FR	25	25	25	25	53.00				30	5	28	46	
Dwarf Koel	*Microdynamis parva*	FR	FR	0	0	50	50	43.00	15							
Buff-faced Pygmy-Parrot	*Micropsitta pusio*	SEFR	FR	0	100	0	0	12.00	18	32						
Forest Honeyeater	*Microptilotis montanus*	FRIN	FR	0	0	100	0	28.00				10	1			
Golden Myna	*Mino anais*	FR	FR	0	0	0	100	148.00	5	18						
Yellow-faced Myna	*Mino dumontii*	FRIN	FR	0	0	0	100	217.00	18	14						
Tit-Berrypecker	*Oreocharis arfaki*	FR	FR	0	0	50	50	22.50				16	3	5	14	
Pheasant Pigeon	*Otidiphaps nobilis*	SEFR	FR	100	0	0	0	500.00			3					
Lesser Bird-of-Paradise	*Paradisaea minor*	FRIN	FR	0	0	0	100	209.25	28	65	65					
Crested Berrypecker	*Paramythia montium*	FR	FR	25	25	25	25	43.50						23	15	80
Hooded Pitohui	*Pitohui dichrous*	FRIN	FR	25	25	25	25	72.00		18	43	17				
Palm Cockatoo	*Probosciger aterrimus*	SEFR	FR	33	0	33	33	770.00	15	12	4					
Brehm's Tiger Parrot	*Psittacella brehmii*	FRVG	FR	0	0	0	100	102.83						2		
Painted Tiger-Parrot	*Psittacella picta*	SEFR	FR	0	50	50	0	58.00						2	8	
Edwards's Fig Parrot	*Psittaculirostris edwardsii*	FR	FR	0	0	0	100	105.00	3	5	10					
Pesquet's Parrot	*Psittrichas fulgidus*	FR	FR	0	0	0	100	745.00	5		8					
Coroneted Fruit-Dove	*Ptilinopus coronulatus*	FR	FR	25	25	25	25	73.67	20	2						
Orange-bellied Fruit-Dove	*Ptilinopus iozonus*	FR	FR	0	0	0	100	110.67	14		20					
Wompoo Fruit-dove	*Ptilinopus magnificus*	FR	FR	25	25	25	25	313.00	11		2					
Ornate Fruit-Dove	*Ptilinopus ornatus*	FR	FR	0	0	0	100	163.00		14	1	2	3			
Pink-spotted Fruit-Dove	*Ptilinopus perlatus*	FR	FR	0	0	0	100	237.33		4						
Beautiful Fruit-Dove	*Ptilinopus pulchellus*	FR	FR	25	25	25	25	71.33	6		2					
White-breasted Fruit-Dove	*Ptilinopus rivoli*	FR	FR	25	25	25	25	148.67				5	19	1		
Superb Fruit-Dove	*Ptilinopus superbus*	FR	FR	25	25	25	25	115.67	2	3	29					
Magnificent Riflebird	*Ptiloris magnificus*	FRIN	FR	0	0	0	100	189.75	2	1	3					
Great Cuckoo-dove	*Reinwardtoena reinwardti*	SEFR	FR	33	0	33	33	256.50	5		2	3	7		2	
Mottled Berryhunter	*Rhagologus leucostigma*	FRIN	FR	0	0	50	50	26.80				10	3	1		
Blyth's Hornbill	*Rhyticeros plicatus*	FRIN	FR	25	25	25	25	1672.50	15	31	1					
Abundances of frugivores									**417**	**414**	**393**	**271**	**186**	**188**	**177**	**92**
Species richness of frugivores									**34**	**31**	**25**	**25**	**22**	**21**	**9**	**4**

HBW_Name	HBW_ScientificName	GuildDetail	Guild	Ground	Low	Middle	Canopy	Mass	200	700	1200	1700	2200	2700	3200	3700
Gray Thornbill	*Acanthiza cinerea*	IN	IN	0	33	33	33	8.40				3	4	28	4	
Papuan Thornbill	*Acanthiza murina*	IN	IN	0	33	33	33	8.40					14	3	14	26
Rufous-naped Bellbird	*Aleadryas rufinucha*	INFR	IN	0	50	50	0	39.90				6	20	6	16	6
Lesser Ground-Robin	*Amalocichla incerta*	IN	IN	100	0	0	0	30.70				1				
Alpine Pipit	*Anthus gutturalis*	INSE	IN	100	0	0	0	35.00								80
Ochre-collared Monarch	*Arses insularis*	IN	IN	0	33	33	33	17.50	4	4		1				
Great Woodswallow	*Artamus maximus*	IN	IN	0	0	0	100	58.20						1	4	6
Chestnut-breasted Cuckoo	*Cacomantis castaneiventris*	IN	IN	50	50	0	0	34.45		2		5	2			
Fan-tailed Cuckoo	*Cacomantis flabelliformis*	IN	IN	0	33	33	33	47.00				10	7	3	4	
White-crowned Koel	*Cacomantis leucolophus*	IN	IN	0	0	0	100	117.00	4	1	17					
Brush Cuckoo	*Cacomantis variolosus*	IN	IN	100	0	0	0	32.40	10	8	4	1				
Obscure Honeyeater	*Caligavis obscura*	INFL	IN	0	33	33	33	26.40			2					
Black-throated Honeyeater	*Caligavis subfrenata*	INFL	IN	0	0	50	50	28.80					1	13	70	2
Golden Cuckooshrike	*Campochaera sloetii*	INFR	IN	0	0	0	100	41.00	1							
Golden Monarch	*Carterornis chrysomela*	IN	IN	0	50	0	50	14.37	11							
Greater Black Coucal	*Centropus menbeki*	INVE	IN	50	50	0	0	334.25	6							
Little Kingfisher	*Ceyx pusillus*	FSIN	IN	0	100	0	0	14.07	1							
Papuan Dwarf Kingfisher	*Ceyx solitarus*	INVE	IN	0	100	0	0	18.50	24	23	1					
Drongo Fantail	*Chaetorhynchus papuensis*	IN	IN	0	50	50	0	34.50			12					
Little Bronze Cuckoo	*Chrysococcyx minutillus*	IN	IN	0	0	0	100	18.50	1							
Rufous-throated Bronze-cuckoo	*Chrysococcyx ruficollis*	IN	IN	0	33	33	33	24.00						1		
Arafura Shrikethrush	*Colluricincla megarhyncha*	IN	IN	25	25	25	25	32.00	14	27	7	13	2			
Arafura Shriketrush	*Colluricincla megarhyncha*	IN	IN	25	25	25	25	21.00				7				
Boyer's Cuckooshrike	*Coracina boyeri*	INFR	IN	0	0	0	100	67.13	1	6	5					
Stout-billed Cuckooshrike	*Coracina caeruleogrisea*	INFR	IN	0	0	0	100	138.50	1	1	35	2	1			
Hooded Cuckooshrike	*Coracina longicauda*	INFR	IN	0	0	0	100	96.50				2		5		
White-bellied Cuckooshrike	*Coracina papuensis*	INFR	IN	33	0	33	33	67.50	13	8	12	1				
Hooded Butcherbird	*Cracticus cassicus*	INVE	IN	0	0	0	100	142.00	27							
Black Butcherbird	*Cracticus quoyi*	INVE	IN	0	0	50	50	159.00	3							
Rusty Mouse-Warbler	*Crateroscelis murina*	IN	IN	100	0	0	0	15.00	1	51	68	2				
Bicolored Mouse-Warbler	*Crateroscelis nigrorufa*	IN	IN	100	0	0	0	15.00			18	3				
Mountain Mouse-Warbler	*Crateroscelis robusta*	IN	IN	100	0	0	0	16.50		2		15	27	30	56	46
Rufous-bellied Kookaburra	*Dacelo gaudichaud*	INVE	IN	50	0	0	50	144.75	29	9						
Black Sittella	*Daphoenositta miranda*	IN	IN	0	50	0	50	14.90							2	
Papuan Sittella	*Daphoenositta papuensis*	IN	IN	0	50	0	50	14.00				2				
Spangled Drongo	*Dicrurus bracteatus*	INFR	IN	0	0	50	50	82.00	12	2	2					
Papuan Cicadabird	*Edolisoma incertum*	INFR	IN	0	0	0	100	56.50	1							
Black Cicadabird	*Edolisoma melas*	INFR	IN	0	0	50	50	59.50	1							
Common Cicadabird	*Edolisoma tenuirostre*	INFR	IN	0	0	0	100	63.67			3					
Brown Sicklebill	*Epimachus meyeri*	INFR	IN	25	25	25	25	210.25				2		28	8	
Papuan Pitta	*Erythropitta macklotii*	IN	IN	100	0	0	0	57.75	3	12						
Garnet Robin	*Eugerygone rubra*	IN	IN	33	33	33	0	8.90				1	12	24	10	10
Wattled Ploughbill	*Eulacestoma nigropectus*	IN	IN	33	33	33	0	21.00						6		
Dollarbird	*Eurystomus orientalis*	INVE	IN	25	25	25	25	161.25	2							
Green-backed Gerygone	*Gerygone chloronota*	IN	IN	0	33	33	33	12.00	6	10	11					
Yellow-bellied Gerygone	*Gerygone chrysogaster*	IN	IN	0	33	33	33	8.00	4	26						
Fairy Gerygone	*Gerygone palpebrosa*	IN	IN	25	25	25	25	8.00	4		4					
Brown-breasted Gerygone	*Gerygone ruficollis*	IN	IN	0	0	100	0					28	26	24	8	4
Torrent-lark	*Grallina bruijnii*	IN	IN	100	0	0	0	38.40				1				
Ashy Robin	*Heteromyias albispecularis*	IN	IN	100	0	0	0	32.00				3	1			
Blue-capped Ifrita	*Ifrita kowaldi*	INFR	IN	25	25	25	25	32.10					2	58	32	2
Black-browed Triller	*Lalage atrovirens*	INFR	IN	0	0	50	50	31.50	1		4					
Black Sunbird	*Leptocoma aspasia*	INFL	IN	0	0	50	50	12.00	27							
Yellow-breasted Boatbill	*Machaerirhynchus flaviventer*	IN	IN	0	33	33	33	10.07	2	1	10	2				
Black-breasted Boatbill	*Machaerirhynchus nigripectus*	IN	IN	0	0	50	50	11.70				30	8	17	6	
New Guinea Scrubfowl	*Megapodius decollatus*	INSE	IN	100	0	0	0	652.00		3						
Lesser Melampitta	*Melampitta lugubris*	IN	IN	100	0	0	0	41.10						10	10	
Belford's Melidectes	*Melidectes belfordi*	INFL	IN	0	0	0	100	64.85				44	48	101	96	4
Ornate Melidectes	*Melidectes torquatus*	INFL	IN	0	0	0	100	44.25				12				
Hook-billed Kingfisher	*Melidora macrorrhina*	INVE	IN	0	0	50	50	95.50	1							
Long-billed Honeyeater	*Melilestes megarhynchus*	INFL	IN	25	25	25	25	41.45	16	25	37	9	2			
Rainbow Bee-eater	*Merops ornatus*	IN	IN	0	0	50	50	27.27	1							
Olive Flyrobin	*Microeca flavovirescens*	IN	IN	33	33	33	0	15.00	9	11	8	1				
Yellow-legged Flycatcher	*Microeca griseoceps*	IN	IN	0	0	50	50	12.80	1		1					
Papuan Flycatcher	*Microeca papuana*	IN	IN	33	33	33	0	14.10				7	25	17		
Mimic Honeyeater	*Microptilotis analogus*	INFR	IN	33	33	33	0	21.00	36	74	16	18	1			
Mountain Honeyeater	*Microptilotis orientalis*	INFL	IN	0	0	0	100	18.00		5	6					
Torrent Flycatcher	*Monachella muelleriana*	IN	IN	100	0	0	0	24.50	4							
Black-winged Monarch	*Monarcha frater*	IN	IN	0	0	0	100	21.00			4					
Shining Flycatcher	*Myiagra alecto*	IN	IN	0	50	50	0	20.00	11							
Spectacled Longbill	*Oedistoma iliolophus*	INNE	IN	0	0	0	100	5.40		3	20					
Piping Bellbird	*Ornorectes cristatus*	IN	IN	50	0	50	0	79.00				2	11	2		
Goldenface	*Pachycare flavogriseum*	IN	IN	0	50	50	0	16.20			3					
Rusty Whistler	*Pachycephala hyperythra*	IN	IN	50	50	0	0	27.70		3	1	15				
Brown-backed Whistler	*Pachycephala modesta*	INFR	IN	0	0	100	0	18.60						6	20	
Regent Whistler	*Pachycephala schlegelii*	INFR	IN	0	50	50	0	22.00				8	52	87	40	2

HBW_Name	HBW_ScientificName	GuildDetail	Guild	Ground	Low	Middle	Canopy	Mass	200	700	1200	1700	2200	2700	3200	3700
Gray Whistler	*Pachycephala simplex*	IN	IN	0	33	33	33	20.50		10	26					
Sclater's Whistler	*Pachycephala soror*	IN	IN	0	50	50	0	24.80		13	20	36	2	4		
White-eyed Robin	*Pachycephalopsis poliosoma*	IN	IN	100	0	0	0	36.25			24	6				
Lowland Peltops	*Peltops blainvillii*	IN	IN	0	0	0	100	30.00	10	3	8					
Mountain Peltops	*Peltops montanus*	IN	IN	0	0	0	100	31.60		11	1		1	4		
White-rumped Robin	*Peneothello bimaculata*	IN	IN	100	0	0	0	23.65		24	14	3				
Blue-gray Robin	*Peneothello cyanus*	IN	IN	100	0	0	0	23.80				94	91			
White-winged Robin	*Peneothello sigillata*	IN	IN	100	0	0	0	22.20						36	58	62
Island Leaf Warbler	*Phylloscopus poliocephalus*	IN	IN	0	0	50	50	9.25			5	51	2			
Northern Variable Pitohui	*Pitohui kirhocephalus*	INFR	IN	25	25	25	25	92.90	7	52	38					
Hooded Pitta	*Pitta sordida*	IN	IN	100	0	0	0	57.00	2	2						
Marbled Frogmouth	*Podargus ocellatus*	INVE	IN	50	50	0	0	167.50				1				
Black-throated Robin	*Poecilodryas albonotata*	IN	IN	0	33	33	33	38.20					2	2	2	
Black-sided Robin	*Poecilodryas hypoleuca*	IN	IN	100	0	0	0	18.00	13	15	4					
Papuan Babbler	*Pomatostomus isidorei*	INVE	IN	50	50	0	0	38.50	3							
Rusty Pitohui	*Pseudorectes ferrugineus*	INFR	IN	25	25	25	25	87.50	16							
Rufous-backed Honeyeater	*Ptiloprora guisei*	INFL	IN	25	25	25	25	22.30				13	38	24	4	
Gray streaked Honeyeater	*Ptiloprora perstriata*	INFL	IN	25	25	25	25	25.10					6	54	92	4
Blue Jewel-babbler	*Ptilorrhoa caerulescens*	INVE	IN	100	0	0	0	49.00	4	6	17					
Chestnut-backed Jewel-babbler	*Ptilorrhoa castanonota*	INVE	IN	100	0	0	0	72.00			4					
Spotted Jewel-babbler	*Ptilorrhoa leucosticta*	INVE	IN	100	0	0	0	50.00				4	5	3		
Forbes's Rail	*Rallina forbesi*	INSE	IN	100	0	0	0	86.25						2		
Friendly Fantail	*Rhipidura albolimbata*	IN	IN	0	33	33	33	10.07				54	64	75	14	
Black Fantail	*Rhipidura atra*	IN	IN	50	50	0	0	11.73			12	39	24	28		
Dimorphic Fantail	*Rhipidura brachyrhyncha*	IN	IN	33	33	33	0	9.45				3	18	64	18	10
Chestnut-bellied Fantail	*Rhipidura hyperythra*	IN	IN		33	33	33	10.75		4						
White-bellied Thicket-Fantail	*Rhipidura leucothorax*	IN	IN	25	25	25	25	18.53	13	3						
Rufous-backed Fantail	*Rhipidura rufidorsa*	IN	IN	25	25	25	25	9.50		4						
Northern Fantail	*Rhipidura rufiventris*	IN	IN	25	25	25	25	16.17	7	8	17					
Sooty Thicket-Fantail	*Rhipidura threnothorax*	IN	IN	100	0	0	0	17.53	13	8	1		3			
Pied Bushchat	*Saxicola caprata*	IN	IN	50	0	0	50	17.55				4	1			
New Guinea Woodcock	*Scolopax rosenbergii*	IN	IN	100	0	0	0	220.00						1		
Large Scrubwren	*Sericornis nouhuysi*	IN	IN	0	50	50	0	14.60				31	87	60	60	10
Papuan Scrubwren	*Sericornis papuensis*	IN	IN	33	33	33	0	10.60				29	13	80	10	
Buff-faced Scrubwren	*Sericornis perspicillatus*	IN	IN	0	50	50	0	9.00				62	51			
Pale-billed Scrubwren	*Sericornis spilodera*	IN	IN	33	33	33	0	11.70		5	1	4		1		
Mountain Kingfisher	*Syma megarhyncha*	INVE	IN	0	0	50	50	53.50			5	18	1			
Yellow-billed Kingfisher	*Syma torotoro*	INVE	IN	25	25	25	25	41.00	2	11		2				
Fan-tailed Monarch	*Symposiachrus axillaris*	IN	IN	0	50	50	0	14.85			8		6			
Spot-winged Monarch	*Symposiachrus guttula*	IN	IN	0	33	33	33	16.13	5	1						
Hooded Monarch	*Symposiachrus manadensis*	IN	IN	33	33	33	0	22.50	11	1						
Common Paradise-Kingfisher	*Tanysiptera galatea*	INVE	IN	100	0	0	0	60.25	6	3						
Forest Kingfisher	*Todiramphus macleayii*	INVE	IN	0	50	50	0	36.80	6	1						
Yellow-bellied Longbill	*Toxorhamphus novaeguineae*	INNE	IN	25	25	25	25	13.90	22	45	34					
Slaty-chinned Longbill	*Toxorhamphus poliopterus*	INNE	IN	25	25	25	25	10.85			12	108	57			
White-faced Robin	*Tregellasia leucops*	IN	IN	33	33	33	0	15.70		1	36					
Island Thrush	*Turdus poliocephalus*	INFR	IN	50	0	0	50	61.95								100
Tawny-breasted Honeyeater	*Xanthotis flaviventer*	INFL	IN	25	25	25	25	38.83	6	24	26					
Black-fronted White-eye	*Zosterops minor*	INFL	IN	25	25	25	25	11.10		20	16					
Abundances of insectivores									**439**	**592**	**640**	**819**	**738**	**908**	**658**	**374**
Species richness of insectivores									**53**	**48**	**48**	**51**	**39**	**36**	**25**	**16**
Pygmy Lorikeet	*Charminetta wilhelminae*	NE		0	0	0	100	34.00		4	19			5		
Papuan Lorikeet	*Charmosyna papou*	NE		0	0	50	100	91.40				47	91	37	42	
Olive-backed Sunbird	*Cinnyris jugularis*	NEIN		0	100	0	0	8.45	3							
Red-capped Flowerpecker	*Dicaeum geelvinkianum*	NEIN		0	0	0	100	6.80	16	57	17	79	16			
Goldie's Lorikeet	*Glossoptila goldiei*	NE		0	0	0	100	53.00				4				
Red-flanked Lorikeet	*Hypocharmosyna placentis*	NE		0	0	50	100	35.57	6	1	36					
Red-fronted Lorikeet	*Hypocharmosyna rubronotata*	NE		0	0	0	100	32.50	1							
Papuan Hanging-Parrot	*Loriculus aurantiifrons*	NEFR		0	0	0	100	14.50	5							
Black-capped Lory	*Lorius lory*	NEFR		0	0	0	100	221.00	28	57	27					
Sooty Melidectes	*Melidectes fuscus*	NEIN		25	25	25	25	68.00						1	16	80
Long-bearded Melidectes	*Melidectes princeps*	NEIN		0	0	0	100	42.00							2	6
Yellow-browed Melidectes	*Melidectes rufocrissalis*	NEIN		0	0	50	50	79.00				47	1	4		
Puff-backed Honeyeater	*Meliphaga aruensis*	NEIN		0	0	0	100	25.40	1	3	3					
Red-collared Myzomela	*Myzomela rosenbergii*	NEIN		0	33	33	33	9.83				118	163	13	42	4
Yellow-billed Lorikeet	*Neopsittacus musschenbroekii*	NE		25	25	25	25	51.50			14	18	1	12		
Orange-billed Lorikeet	*Neopsittacus pullicauda*	NE		0	0	0	100	32.43				33	5	63	16	
Plum-faced Lorikeet	*Oreopsittacus arfaki*	NE		0	0	0	100	20.73				2		33	86	8
Helmeted Friarbird	*Philemon buceroides*	NEIN		0	0	50	50	177.00	32	1		1				
Meyer's Friarbird	*Philemon meyeri*	NEIN		0	33	33	33	52.90	25	10	7					
Dusky Lory	*Pseudeos fuscata*	NE		0	0	0	100	152.67	21			67	133			
Plain Honeyeater	*Pycnopygius ixoides*	NEIN		0	33	33	33	25.75	2	1		3				
Coconut Lorikeet	*Trichoglossus haematodus*	NE		0	0	50	50	118.00	34	48	16					
New Guinea White-eye	*Zosterops novaeguineae*	NEIN		33	33	33	0	12.50		5		19	31	2		
Red-legged Brushturkey	*Talegalla jobiensis*	OM		100	0	0	0	1559.00	13	2	4					
Blue-faced Parrotfinch	*Erythrura trichroa*	GR		50	50	0	0	10.80				13	1	4	8	4
Streak-headed Munia	*Mayrimunia tristissima*	GR		50	50	0	0	15.00				2	1			

Table S5. List of recorded bats and their feeding specializations. Bat species acoustically recorded along the Mt. Wilhelm gradient. Numbers represents the relative abundance calculated from the recordings. Feeding guilds and foraging habits come from the literature (Flannery 1995, Bonaccorso 1998, Zachos et al. 2020).

Species	**Call type**	**200**	**700**	**1,200**	**1,700**	**2,200**	**2,700**	**3,200**	**3,700**	**Food**	**Foraging**
HIPPOSIDERIDAE											
Hipposideros wollastoni	84 mCF					22				Likely insects	NA
Hipposideros cervinus	140 sCF	2								Beetles, moths and other insects	Aerial and gleaning
EMBALLONURIDAE											
Emballonura beccarii / Mosia nigrescens	62 i.fFM.d	12	16	10	1					Beetles, wingless ants	Aerial and gleaning
Emballonura beccarii / Mosia nigrescens	72 i.fFM.d	12									
VESPERTILIONIDAE											
Pipistrellus papuanus	48 st.cFM	10								Aerial insects	Hawker
Nyctophilus microtis	45-50 bFM	5	4	1						Insects	Likely aerial and gleaning
MINIOPTERIDAE											
Miniopterus tristis / Pipistrellus collinus	38 st. cFM							11		Aerial insects	Hawker
Miniopterus sp. 1 'medium'	43 st.cFM	9	11			7	2			Likely insects	NA
Miniopterus australis [=*Miniopterus* sp. 2 ‘small’]	54 st.cFM	5	1				39	13	4	Flies, ants, moths and wasps	Hawker
MOLOSSIDAE											
Austronomus kuboriensis	13 cFM		5				3			Beetles	Hawker
Otomops secundus	18 cFM						1			Beetles, aerial insects	Hawker
Total species richness		7	5	2	1	2	4	2	1		
Total relative abudances		55	37	11	1	29	45	24	4		

Table S6. Average increase of abundances of all arthropods in predator exclosures in wet and dry season at the surveyed elevational study sites based on the raw data (a) and based on the estimates predicted by the best model (b). Emmean estimates (below diagonal) and pairwise contrasts (above diagonal) for the treatments irrespective to the season and elevation. Treatments: VER = insectivorous vertebrates excluded, ALL = both insectivorous vertebrates and ants excluded, ANT = ants excluded, CON = control treatment to which the abundances of arthropods in predator exclosures were related.

a)		Abundance increased by % (Raw data)			b) Abundance increased by % (3700 Model)		
		VER	ALL	ANT	VER	ALL	ANT
Wet season	200	39.27	36.86	3.70	39.86	22.55	3.28
	700	58.72	17.76	10.29	32.41	22.99	6.39
	1200	58.90	38.09	20.03	27.48	24.40	9.13
	1700	30.21	44.97	6.02	24.60	26.89	11.77
	2200	37.88	44.69	25.68	23.67	30.81	14.54
	2700	92.85	74.99	16.12	24.99	36.84	17.77
	3200	73.26			29.51		
	3700	77.15			39.82		
Dry season	200	54.66	28.58	7.64	68.41	38.68	5.62
	700	13.96	14.02	-9.24	48.74	34.55	9.59
	1200	33.35	34.24	14.70	37.98	33.71	12.61
	1700	48.17	29.03	4.97	32.21	35.20	15.40
	2200	-4.67	19.14	-16.95	30.04	39.09	18.44
	2700	25.39	38.19	14.45	31.41	46.31	22.33
	3200	31.63			37.77		
	3700	10.74			54.56		

c)

	CON	ANT	VER	ALL
CON	X	0.390	**0.003**	**0.002**
ANT	-3.179	X	0.354	0.233
VER	**-6.484**	-3.305	X	0.985
ALL	**-7.204**	-4.024	-0.719	X

Table S7. Average increase of herbivory chewing damage in predator exclosures in wet and dry season at the surveyed elevational study sites based on the raw data (a) and based on the estimates predicted by the best model (b). Emmean estimates (below diagonal) and pairwise contrasts (above diagonal) for the treatments irrespective to the season and elevation. Treatments: VER = insectivorous vertebrates excluded, ALL = both insectivorous vertebrates and ants excluded, ANT = ants excluded, CON = control treatment to which the abundances of arthropods in predator exclosures were related.

a)		Increased by % (Raw data)			Increase by % (3700 Model)		
		VER	ALL	ANT	VER	ALL	ANT
Wet season	200	230.30	242.87	123.17	22.13	42.38	28.15
	700	70.50	66.59	5.49	19.30	28.87	16.46
	1200	-26.02	8.06	60.80	21.00	23.79	8.19
	1700	-17.75	-22.66	-28.54	27.46	26.28	2.76
	2200	85.65	59.03	140.33	39.51	36.92	-0.18
	2700	114.04	102.33	-51.60	58.71	57.87	-0.81
	3200	118.11			87.74		
	3700	100.00			130.96		
Dry season	200	-3.94	29.90	0.42	22.35	42.88	28.45
	700	7.33	-14.97	40.68	19.47	29.16	16.62
	1200	23.47	24.98	-5.84	21.16	23.98	8.27
	1700	250.05	114.17	87.01	27.64	26.46	2.79
	2200	35.99	72.64	36.19	39.73	37.12	-0.18
	2700	66.67	193.78	34.95	59.01	58.15	-0.81
	3200	159.82			88.13		
	3700	554.72			131.46		

c)

	CON	ANT	VER	ALL
CON	X	0.743	**0.001**	**0.003**
ANT	-1.011	X	**0.062**	0.083
VER	**-3.761**	**-2.487**	X	1.000
ALL	**-3.447**	-2.373	0.001	X

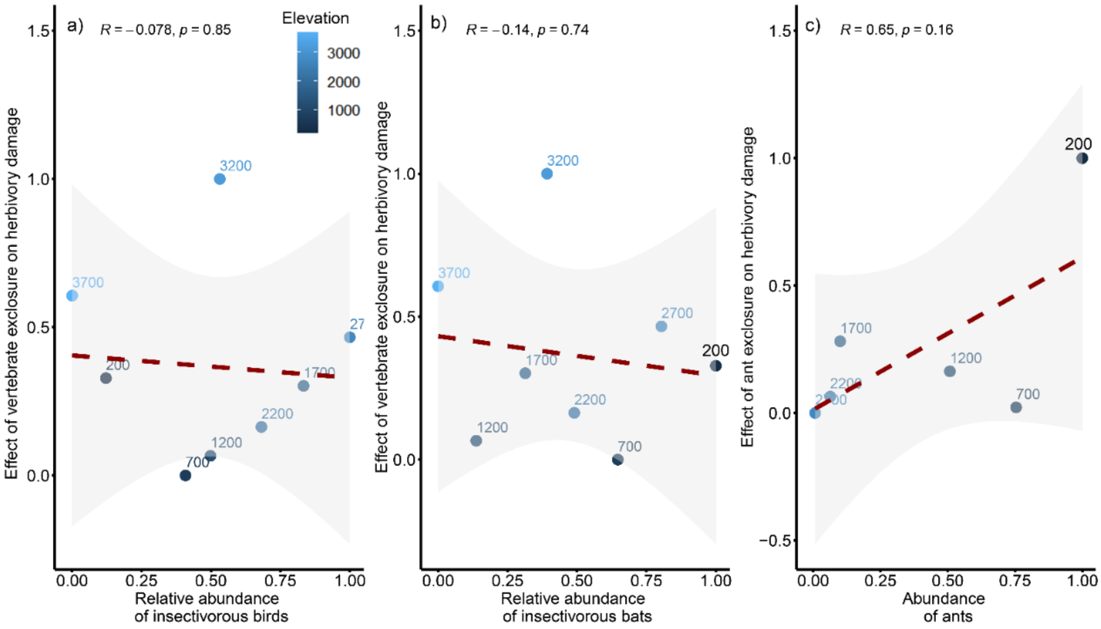

Figure S2. Correlations between effect of vertebrate (a, b) and ant (c) exclosure (LRR calculated from raw data, normalized data) on herbivory caused by chewing arthropods (a, b, c).

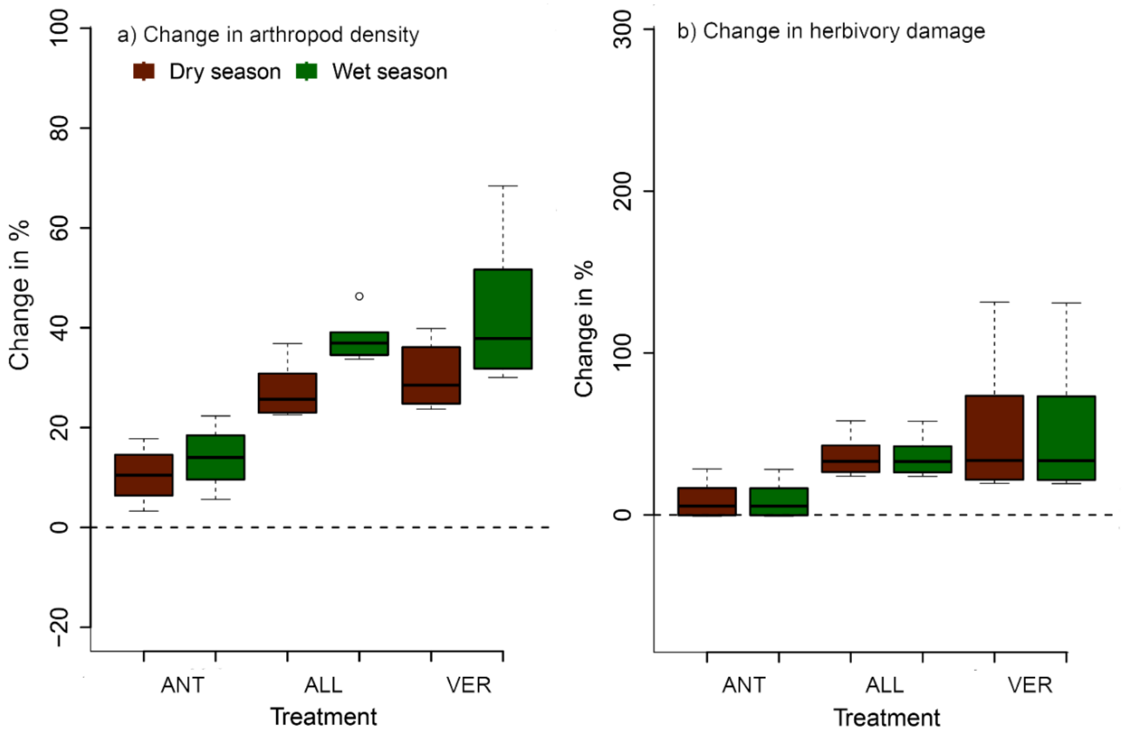

Figure S3. The overall *predicted* (by the best models) changes in the arthropod densities (a) and herbivory damage (b) in wet and dry season (marked by colour) after the predators were excluded, irrespective to elevation. Zero change (marked by a dashed line) means that the arthropod density or herbivory damage did not change from the respective control treatment. Values below 0 mean that the respective value was higher at control tree than in predator exclusion treatment. Treatments: ANT = saplings from which ants are excluded by tanglefoot glue, VER = saplings from which insectivorous vertebrates were excluded by cages, ALL = saplings from which both ants and insectivorous vertebrates were excluded. Boxplots are showing medians, 25 and 75% quartile, maxima, and minima. Outliers are marked by empty circle. Figure S3 is based on values predicted by the best models, while Figure 1 shows the actual change in densities and herbivory (i.e., raw data). See also Table S6 and S7 for details.

Table S8. Corrected Akaike Information Criterion (AICc) of regression models examining as mean body size of arthropods per sapling (mean; N = 1092) and as body size measurements of all individuals (full; N = 32,341), log-transform them. Best considered models are marked by shade in the cell.

	Body sizes (mean)		Body sizes (full)	
	dAICc	df	dAICc	df
Null	162.2	4	454.7	4
Treatment	86	7	401.7	7
Elevation	129.8	6	419.5	6
Season	167.1	5	440.1	5
Treatment + Season	90.9	8	387.4	8
Treatment + Elevation	48.1	9	361	9
Season + Elevation	90.9	8	387.4	8
Treatment : Season	93.9	11	347.8	11
Treatment : Elevation	89.6	12	327.8	12
Season : Elevation	106.7	8	131.2	8
Treatment : Season + Elevation	56	13	307.4	13
Treatment : Elevation + Season	94.6	13	313	13
Season : Elevation + Treatment	24.9	11	72.4	11
Treatment + Elevation + Season	53	10	346.9	10
Treatment + Elevation + Season + Treatment : Elevation	23.3	16	279.5	16
Treatment + Elevation + Season + Treatment : Season	56	13	307.4	13
Treatment + Elevation + Season + Elevation : Season	29.8	12	67.5	12
Treatment + Elevation + Season + Elevation : Season + Elevation : Treatment	0	18	1.2	18
Treatment + Elevation + Season + Elevation : Treatment + Season : Treatment	26.3	19	240.6	19
Treatment + Elevation + Season + Elevation : Treatment + Season : Treatment + Season : Elevation	8	21	0	21

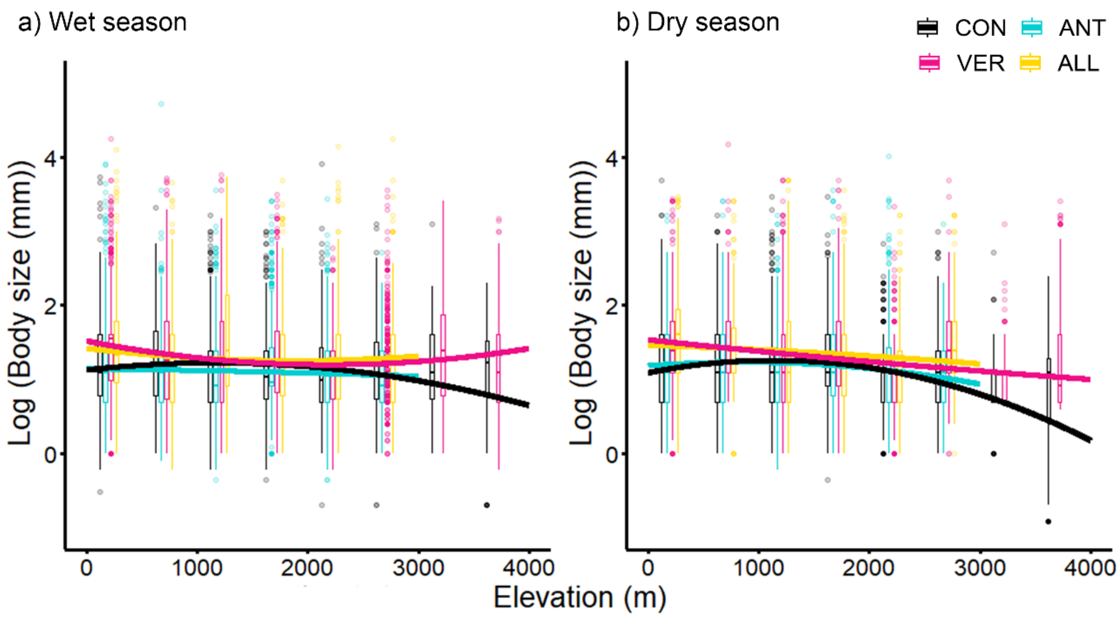

Figure S4. Effect of the predator exclusion on the body size of all arthropods collected from saplings along the elevational gradient of Mt Wilhelm in the wet (a) and dry season (b) when body size of all individual arthropods is considered. The curves show predicted values from the best linear model which included season, elevation, and treatment as a fixed factor. See Table S8 for model results. Boxplots (a, b) are showing medians, 25 and 75% quartile, maxima, and minima. See Table S8 for the best model.

Chapter 3

Birds and bats reduce herbivory damage in Papua New Guinean highland forests

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Birds and bats reduce herbivory damage in Papua New Guinean highland forests

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Abstract

Insectivorous predators, including birds and bats, play crucial roles in trophic cascades. However, previous research on these cascades has often relied on permanent predator exclosures, which prevent the isolation of specific effects of birds and bats, given their different activity patterns throughout the day. Moreover, limited knowledge exists regarding the variations in individual effects of these predators under different biotic and abiotic conditions, such as changes in elevation. To address these uncertainties, our study aimed to investigate the distinct effects of bats and birds on arthropod densities in foliage and herbivory damage in lowland and highland rainforests of Papua New Guinea (PNG). Predator exclosures were established for one month to exclude diurnal or nocturnal predators across 120 saplings (ca. 2.5-4 m tall) selected from two lowland and two highland forests (i.e., 30 saplings per study site) along the Mt. Wilhelm transect in PNG. Arthropods were collected and measured, and herbivory damage was analysed at the end of the experiment. Birds significantly reduced arthropod densities by 31 %, particularly in arthropods longer than 10 mm, regardless of elevation. Additionally, both birds and bats appeared to mitigate herbivory damage in highland forests, with protected saplings displaying up to 189 % more herbivory. Consequently, establishing a clear relationship between arthropod densities, herbivory, and vertebrate insectivores was challenging due to the complexity of tropical rainforest food webs. Nonetheless, we provide recommendations for future exclosure experiments to unravel the context-specific nature of trophic cascades in natural ecosystems.

Introduction

Trophic interactions play a crucial role in maintaining balance and promoting diversity in natural ecosystems (Aoki & Mizushima, 2001; Thébault & Loreau, 2005). Predation along with competition are good examples of how trophic interactions can maintain and enhance diversity, by regulating prey populations and preventing any one species from becoming dominant (Chase et al., 2002; Chesson et al., 2008). However, predator populations are declining primarily because of factors such as unsustainable hunting (Benítez-López et al., 2017), habitat fragmentation (Morante-Filho et al., 2016; Şekercioḡlu et al., 2002) and climate change (Şekercioḡlu et al., 2012; Laws, 2017). Therefore, a comprehensive understanding of prey-predator interactions is absolutely crucial for predicting the impacts of human activities on ecosystems (Morante-Filho et al., 2016; Schulze et al., 2012). A common method to study prey-predator interactions, and their impact on plants, is to manipulate the top of the trophic chain using predator exclosure experiments (Maas et al., 2019).

Existing predator exclosure experiments have demonstrated that both bats and birds, as predators of arthropods, play vital roles in ecosystem functioning, and their exclusion (i.e., the absence of predators) can lead to significant changes in the ecosystem (Maas et al., 2016). Indeed, they demonstrated the ability to reduce the total abundance and biomass of arthropods in tropical, as well as temperate ecosystems (Böhm et al., 2011; Johnson et al., 2010; Karp et al., 2014; Maas et al., 2013; Mooney et al., 2010; Nyffeler et al., 2018). Via top-down control, predators reduce densities of herbivorous arthropods which consequently results in lesser damage to plants (Kalka et al., 2008; Morrison & Lindell, 2012; Van Bael et al., 2003). However, most of the predator exclosures have been constructed as permanent structures, confounding the effect of birds and bats (Houska Tahadlova et al., 2023; Philpott et al., 2004; Sam et al., 2023). Moreover, the majority of the experiments occurred in agricultural systems (Cassano et al., 2016; Ferreira et al., 2023; Karp et al., 2014; Maas et al., 2013; Schmitt et al.,

2021) from temperate, neotropical and Caribbean zones (Maas et al., 2016; Maas et al., 2019). The emphasis on the agricultural context primarily arises from the threat posed by herbivorous insects to agricultural commodities. However, the emergence of herbivorous insect populations, driven by a decrease in predation by birds and bats, can also have significant repercussions for natural ecosystems, especially forest ecosystems, which are inherently less adaptable compared to managed agricultural or artificial ecosystems. Unlike in agriculture, where management responses can involve altering host plant assemblages entirely, forests remain largely fixed in their location (Logan et al., 2003). For instance, insect outbreaks can alter the species composition of forests (Ayres & Lombardero, 2000; Jactel et al., 2021) which can in turn have detrimental effects on essential ecosystem processes such as water flow and carbon flux (Shukla et al., 1990; Griffiths et al., 2021). Therefore, it is crucial to gain a deeper understanding of trophic cascades within natural ecosystems as well.

The effects of bird and bat communities on arthropods and indirectly on plants can vary greatly because of differences in species richness, functional richness, and relative abundance across different locations. Bat and bird species have different prey preferences (e.g., Lepidoptera, Coleoptera) and foraging strategies (e.g., gleaning, hawking) that may significantly change the consequences on plants (i.e., for instance, if herbivorous insects are preferred). The effect of the predators is also size-dependent, as the predators prefer prey of a specific size. Indeed, insectivorous birds and bats mainly targeted large arthropods (>3 mm) according to earlier studies (Philpott et al., 2004; Van Bael et al., 2003). The rare studies looking for the individual effects of bats and birds have found that both are equally important (Morrison & Lindel, 2012) or that a relative individual effect of bats and birds differs between localities (Kalka et al., 2008; Karp & Daily, 2014), seasons (Williams-Guillén et al., 2008) or landscape context (Maas et al., 2013). Despite the low number of studies, the existing data indicate that the individual effects of birds and bats on arthropod communities are likely to be site-specific because of differences in species and functional richness.

In addition to consuming herbivorous arthropods, both bats and birds are known to engage in intraguild predation, preying on mesopredators such as spiders and ants that occupy a niche between top predators and smaller prey (Gunnarsson, 2007; Karp et al., 2014; Maas et al., 2013; Philpott et al., 2004). In that case, the positive effects of predation on arthropod herbivores can be counterbalanced by the negative effects of intraguild predation suppressing mesopredator populations, thus modifying the net effect of vertebrate predators on arthropod abundances and consequences for plants (Mooney et al., 2010; Schmitt et al., 2021). Nevertheless, limited information is available about the strength of intraguild predation in trophic cascades, especially for birds and bats individually.

Elevational gradients are excellent systems to better understand natural processes such as trophic interactions (Moreira et al., 2018). Increasing elevation induces variation in abiotic factors such as nutrient availability, sunlight, and climatic factors (e.g., temperature, precipitation), indirectly leading to changes in bat, bird, plant, and arthropod communities (e.g., species richness, functional richness, abundances) (Colwell et al., 2016; Moreira et al., 2018). While the diversity and relative abundance of plants, insect herbivores, and predators generally decline with increasing elevation, there is variation in this pattern among taxa (McCain et al., 2010), spatial scale, mountain ranges in different climatic regimes (McCain, 2009; McCain et al., 2010) or even within the same mountain (Colwell et al., 2016). Broad generalizations are not yet possible along elevations. Therefore, this study aimed to provide an initial understanding of how trophic cascades vary in response to changes in biotic and abiotic conditions resulting from changes in elevation.

We explored the individual effects of birds and bats in the lowland and highland forests of Papua New Guinea. For that, we ran predator exclosure experiments at four natural forest study sites along the well-studied Mt. Wilhelm elevational transect (Robillard et al., 2016; Sam et al., 2019; Sam et al., 2020; Sivault et al., 2023; Souto-Vilarós et al., 2020; Szczepański et al., 2018) and aimed to answer: (1) Do bat and bird exclosures affect densities of arthropods in highlands and lowlands equally? After the removal of vertebrate predators, we expect a greater increase in the arthropod densities at the lowland study sites because of the higher richness of bats and birds at low elevations. (2) Are arthropods of all body sizes and feeding guilds affected equally? We expect herbivorous and predatory arthropods to be the most affected feeding guilds by the removal of vertebrate predators as well as large arthropods (3) Does the absence of birds and bats translate indirectly to a change in herbivory damage? We expect that the consumption of both mesopredators and herbivores by birds and bats will counterbalance or weaken the trophic cascades and will result in small differences in herbivory damage between treatments, at least in some study sites.

Methods

Study sites and plant species

We conducted the predator exclosure experiments during the dry season between 2-Apr-2015 and 25-Jun-2015 at four elevational study sites of the Mt. Wilhelm elevational gradient in Papua New Guinea. The “El Niño” phenomenon did not affect the experiments as it started later in 2015. The first two sites, so-called “lowland” sites, were located at 200 and 700 m a.s.l. and described by Paijmans (1975) as typical lowland alluvial and foothill forests, respectively. The two other sites, so-called “highland” sites, were located at 2200 and 2700 m a.s.l. and described as lower montane forests. Mean daily temperatures are 24.5 °C and 22.3°C at 200 and 700 m a.s.l. respectively, and 15.6°C and 13.1°C at 2200 and 2700 m a.s.l. (Sam et al., 2019). Mean annual precipitation is 3,288 mm in the lowlands, rising to 4,400 mm at the timberline, with a condensation zone between 2,500 and 2,700 m a.s.l. (Sam et al., 2019).

Unfortunately, no common tree species occur at all four elevational study sites. Thus, we selected tree species typical for the understory of each of the study sites that do not have extreme defences or associations with ants, five tree species in lowland and six in highland study sites (11 tree species in total) (Appendix S1: Table S1). We ran the experiment on *Cleistanthus myrianthus* (Phyllanthaceae), *Gymnacranthera paniculate* (Myristicaceae), and *Syzygium thomei* (Myrtaceae) at both 200 and 700 m a.s.l. with *Ficus conocephalifolia* (Moraceae) as an additional species at 200 m. While we used *Garcinia scretaria* (Clusiaceae), *Litsea tomiriana* (Lauraceae), and *Pouteria microphorta* (Sapotaceae) at both 2200 and 2700 m with *Schuurmansia elegans* (Ochnaceae), *Symplocos cochinchinensis* (Symplocaceae), *Syzygium benjaminum* (Myrtaceae) as additional species at 2200 m and, *Nothofagus grandis* (Nothofagaceae) as an additional species at 2700 m to reach similar sample size at each elevational study site.

Experimental design

We preselected saplings with approximately 500 leaves growing within a well-developed crown 2.5 – 4 m above the ground without any arthropod nests or abnormally high herbivory or fungal damage. Average leaf sizes of the selected tree species ranged from 13.47 to 502.37 cm2 (mean ± S.E. = 113.12 ± 51.4). Before setting up the exclosures, all arthropods were meticulously removed by shaking them off the saplings. This was done to standardize the starting position of the treatments, as the saplings assigned to the predator exclosures were inevitably shaken during the exclosure construction. Based on our experience, recolonization of the saplings by arthropods takes ca. 3 days.

Using predator exclosures constructed from PVC tubes and agricultural nylon netting (mesh size 3 cm, Sam et al., 2023), we excluded birds and bats from saplings individually and accompanied them with control saplings (Fig. S1a). Namely, each sapling was assigned to one of the three treatments – bird exclosure, bat exclosure, and control. In total, we worked on 30 individual saplings per elevational site. We balanced the number of saplings used for each treatment per plant species (Table S1) with at least a minimum of 10 m between the saplings, with saplings randomly distributed across a forest area of ca. 12 ha. To exclude the birds or bats individually, mobile exclosures hanging on ropes attached to canopy trees were protecting the respective 20 saplings at each of the four elevational study sites (Fig. S1a). Ten of them were diurnal exclosures preventing access of birds, pulled down (to cover the crown completely) at sunrise and up (1 m above the crown of the sapling) at dusk. Ten of them were nocturnal exclosures preventing access to bats, pulled up at sunrise, and pulled down at dusk. The exclosures were pulled twice a day daily for one month (31±3 days) at each study site.

Arthropod collection

After one month of the treatments, exclosures were removed carefully (i.e., by pulling them up), and the trunk of the sapling was slowly lowered above a 2x2 m large mosquito net (Fig. S1b), all foliage was quickly wrapped to the net, and sprayed by fast knock-down insecticide (Mortein®). After a while, we shook foliage firmly, opened the net, collected all arthropods (>1mm), and preserved them in vials filled with DNA-grade ethanol. We then checked the leaves for arthropods which did not drop.

In the laboratory, all arthropods were identified into orders or families, and four feeding specializations (i.e., leaf chewers, mesopredators, "non-related" and sapsuckers) following Tahadlova *et al.* (2023) and Sam *et al.* (2023) and measured to nearest 0.1 mm (Table S2). Arthropods listed in the "non-related" (NR) represent feeding specialization which has no impact on plant damage or other arthropods. The life stage was considered for the identification of the feeding guilds. We then calculated arthropod densities per m^2 of foliage by dividing the arthropod abundances collected from each sapling by the total leaf area of the given sapling (i.e., described hereafter).

Herbivory measures

To assess herbivore damage, we randomly selected two branches of each sapling (with ca. 50 leaves in total), collected, and weighted all the leaves from them. Using a 50 x 50 cm^2 white background, we took photographs of spread and flattened leaves collected from these two branches to calculate the leaf area of the subsample (Fig. S1c). We then weighed all the remained leaves on the sapling. By the weight of the leaves from the selected branches and the complete sapling, we obtained an estimation of the number of leaves which allowed us to calculate an approximation of the total leaf area of each sapling.

Using Adobe Photoshop CS6 (Adobe Systems Inc., USA), we outlined the missing edges on the ca. 50 photographed leaves, based on their 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 estimated the percentage of leaf area loss as c/b x 100, hereby defined as herbivory damage in cm^2 per 100 cm^2 of foliage.

Vertebrate predators

To compare the experimental outcomes with the richness and abundance of vertebrate predators, we incorporated bird data that had been surveyed both before (September – October 2013) and after (October – December 2015) the exclosure experiment, as well as bat data surveyed before the exclosure experiment (February–July 2015) at the same study sites. We included the earlier bird data from 2013 due to the likelihood of the 2015 survey being affected by El Niño, as noted by Sam et al. (2022). The methods and data about birds were published separately in several studies (Marki et al., 2016; Sam et al., 2019; Sam et al., 2023), as were those for bats (Sivault et al., 2023; Sam et al., 2023).

For this study, we exclusively extracted information on the abundances and species richness of insectivorous birds found in the understory, utilizing the point-counts technique, and classifying them as insectivores or partly insectivores based on dietary information gathered from literature (Billerman et al., 2022) and previous sampling efforts (Sam et al., 2017). Similarly, only bat species detected using active acoustic detection and identified as strict insectivores based on existing literature (Bonaccorso, 1998; Flannery, 1995) were considered for this study.

We further categorized bird and bat species according to their foraging behaviour, distinguishing between gleaners and other foraging types (such as hawkers), relying on K. Sam's personal observations, the birdsoftheworld.org database, as well as references provided by Bonaccorso (1998), Flannery (1995), and Zachos (2020) (Table S3 and S4). Nevertheless, it is worth noting that both bats and birds have demonstrated some flexibility in their foraging strategies (Scott et al., 2003; Pavey & Burwell, 2000), which may introduce some variability into these categories.

Shortly, the gleaning bat species were found at the two lowland study sites, while bat aerial hawkers were present at all study sites except for the one at 2,200 m (Figure 1a). We lacked foraging information for bats at the 2,200 m elevation, although they were identified as *Hipposideros wollastoni* and *Miniopterus sp.*, with the most abundant species, *H. wollastoni*, likely employing a gleaner strategy based on the behaviour of other Hipposideros species worldwide (Wilson, 1973). Most of the insectivorous bird species observed at the study sites were gleaners (Figure 1b). The relative abundance of bats was the highest at the lowest (200m) and the highest (2,700m) study sites, with predominantly gleaners in the lowlands and hawkers in the highlands (Figure 1c). On the other hand, the relative abundance of birds increased from the lowland to the highland study sites, with a clear majority of gleaners in all sites (Figure 1d).

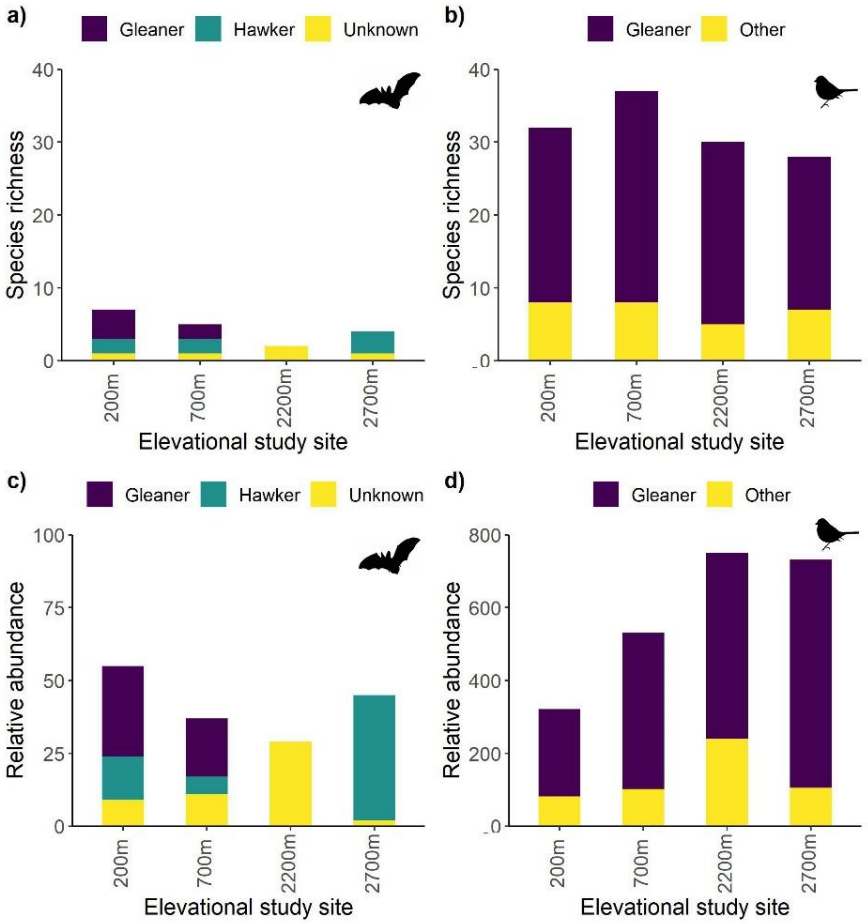

Figure 1. Bar charts of the species richness (a) and the relative abundance (c) of bats according to their foraging habits (i.e., gleaner, hawker, and unknown (NA)) and of the species richness (b) and relative abundance (d) of birds according to their foraging habits (i.e., gleaner or other) at the four elevational study sites (i.e., 200, 700, 2200, 2700).

Statistical analysis

We first built linear mixed models following a Gaussian distribution using the package “lme4” (Bates et al., 2015) to test the effect of treatment and elevation on the total arthropod densities (number of individuals per m² of foliage), the arthropod sizes and the arthropod densities partitioned in four feeding guilds: chewers, mesopredators, sapsuckers and NR (non-related).

The models contained the variable treatment (factor of 3 levels), elevation (factor of 4 levels), and their interaction. Plant species (factor of 11 levels) were used as a random effect in the models. The arthropod densities and sizes were standardized (Z-scores) using the R function “scale” before the analyses. Then, we ran generalized linear mixed models ‘glmmTMB’ (Brooks et al., 2017) using a beta error distribution to determine the effect of treatment and elevation on the herbivory damage (the proportion of the leaf area lost per 100 cm^2 of foliage). Similarly, the models contained the variable treatment, elevation, and their interaction with plant species as a random effect.

To select the best models, we used the AICctab function from the bbmle package (Bolker et al., 2017), which computes the information criteria of all our models using parsimony (AICc) (Table 1). When the most parsimonious model was picked based on the AIC, we controlled the model fit with the “Dharma” package (providing diagnostic plots of the residuals) (Hartig et al., 2017) and ran an analysis of variance. For the best models, we obtained estimated marginal means (= emmeans) and comparisons among all variable levels, using the emmeans package (Lenth et al., 2018). All analyses were conducted in R version 4.1.0 (R Core Team, 2020).

Table 1: Corrected Akaike Information Criterion (AICc) of linear and generalized mixed models examining densities of all arthropods, sizes of all arthropods, herbivory damage and densities of arthropods partitioned in four feeding guilds (i.e., chewer, mesopredator, sapsucker and NR), after exclusion of vertebrate predators (treatment) at four elevational study sites of Mt. Wilhelm (elevation) in Papua New Guinea. Most parsimonious models are in bold.

	Arthropod densities		Arthropod sizes		Herbivory damage	
	dAICc	df	dAICc	df	dAICc	df
Null	3.0	3	59.2	3	22.8	3
Treatment	**0.0**	**5**	51.6	5	3.8	5
Elevation	8.5	6	43.9	6	22.6	6

Treatment + Elevation	5.8	8	36.7	8	3.5	8
Treatment + Elevation + Treatment : Elevation	14.0	14	**0.0**	**14**	**0.0**	**14**

	Chewer densities		Mesopredator densities		Sapsucker densities		NR densities	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Null	4.2	3	3.4	3	19.8	3	5.5	3
Treatment	**0.0**	**5**	**0.0**	**5**	18.1	5	3.0	5
Elevation	7.9	6	4.8	6	18.1	6	2.5	6
Treatment + Elevation	4.0	8	1.6	8	16.2	8	**0.0**	**8**
Treatment + Elevation + Treatment : Elevation	7.1	14	9.2	14	**0.0**	**14**	6.9	14

Results

Arthropod densities

In total, we collected 3,245 arthropods from 120 tree saplings at four elevational study sites at the end of the one-month-long predator exclusion experiment. Only treatment had a significant effect on the resulting total densities of all arthropods (X_2 = 7.39, df = 2, P = 0.02, Table 1, Figure 2a). In the absence of birds, the arthropod density increased significantly (z = 2.71, P = 0.02), by 31 % in comparison to the control saplings. The effect of bats was detectable (i.e., an increase of arthropod densities by 15 % in comparison to the control saplings) but not significant (z = 1.3, P = 0.39).

To determine which type of arthropods (i.e., chewer, mesopredator, sapsucker, and non-related arthropods) are affected the most, we tested vertebrate predator’s effect on them separately. Only treatment had a significant effect on the density of chewers (X_2 = 8.84, df = 2, P = 0.01, Figure 2b). While the absence of birds led to a significant increase in the density of chewers by 70 % (z = 2.92, P = 0.01), the effect of bats was detectable (i.e., an increase of chewers by 42 % in bat exclosures) but non-significant (z = 1.75, P = 0.19) (Table S5). The leaf-chewing arthropods were primarily represented by caterpillars, herbivorous orthopterans and beetles (Chrysomelidae and Curculionidae) (Table S2).

The density of mesopredators (mainly represented by spiders and ants, Table S2) was affected by the treatments as well (X_2 = 8.01, df = 2, P = 0.01, Figure 2c). Bird exclusion led to a significant increase of mesopredator densities by 41 % (z = 2.77, P = 0.01) whereas the effect of bats was detectable (i.e., an increase of mesopredators by 15%) but not significant (z = 1.02, P = 0.56) (Table S5).

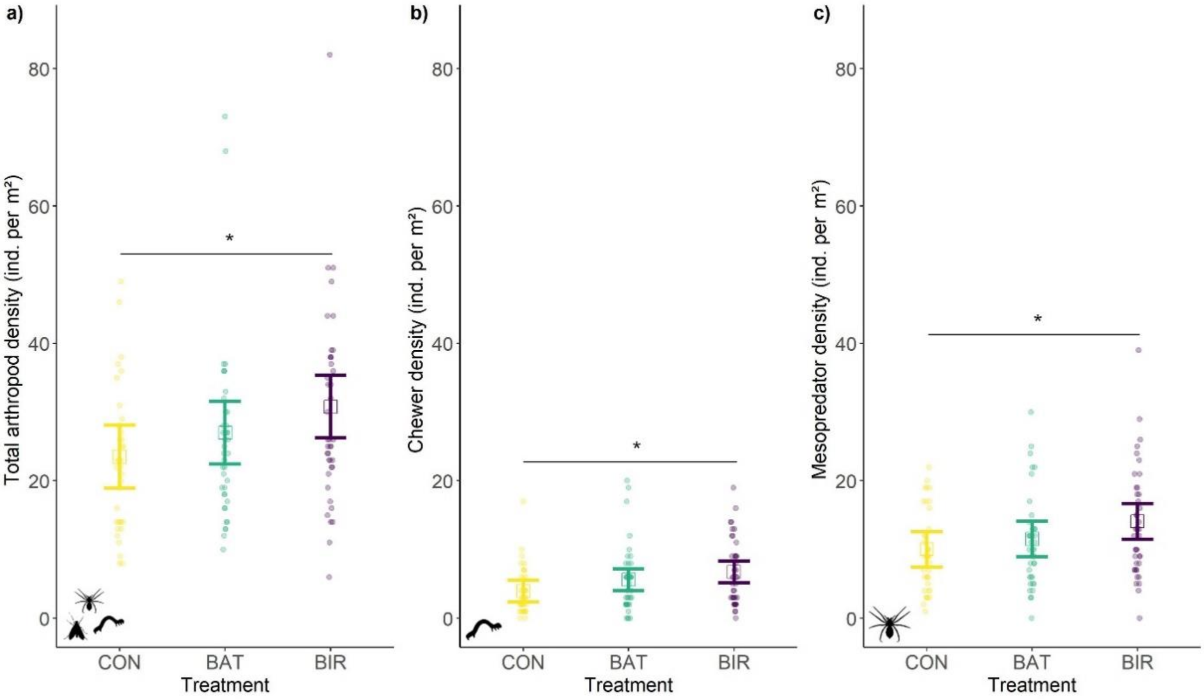

Figure 2. Effect of treatment (CON=control, BAT=bat exclosure, BIR=bird exclosure) on the total arthropod (a) chewer (b), mesopredator (c) densities per square meter of foliage summarized across the four study sites. Estimated marginal means ± confidence intervals are plotted by square and whiskers and means per sample at each elevation are plotted by small dots. Significance is marked as follows: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001, NS P > 0.05.

Treatment had a significant effect on the sapsucker densities (mostly Hemipterans, Table S2) only in interactions with elevation (X_2 = 35.23, df = 6, P <<0.001, Fig. S2). Specifically, bat and bird exclosures significantly decreased the sapsucker densities at 700m by 87 % and 81 %, respectively, in comparison to control saplings (z = 5.54, P < 0.001; z = 5.12,

$P < 0.001$; respectively) (Table S5). None of the other study sites showed a significant response to treatment on sapsucker densities.

Finally, treatment and elevation had a significant effect on the non-related (NR) arthropods ($X_2 = 7.22$, df = 2, $P = 0.02$; $X_2 = 12.94$, df = 3, $P = 0.004$, respectively). Birds significantly suppressed NR arthropods in all study sites ($z = 2.48$, $P = 0.03$; from an increase of 50 to 193 % of NR arthropods in bird exclosures; Table S5) whereas bats did not affect them at any of the sites ($z = 0.51$, $P = 0.86$) (Fig. S3).

Arthropod sizes

The body sizes of arthropods from our saplings varied from 1 to 89 mm with a median size of 3 mm (mean = 4.07). Specifically, the control saplings hosted arthropods between 0.4 to 40 mm long. We found no difference in arthropod abundances between the predator-protected saplings and the control saplings, for body size classes up to 11 mm. Above 11 mm, larger arthropods surviving in the predator exclosures were more abundant than in the foliage of control saplings (Fig. S4).

Elevation in interaction with treatment had a significant effect on the total arthropod sizes ($X_2 = 49.12$, df = 6, $P <0.001$) (Figure 3). The exclusion of birds significantly increased the size of the arthropods by 0.2 mm collected at 200m in comparison to control saplings ($z = 2.59$, $P = 0.02$). While at 700m, both the exclusion of birds and bats led to an increase of the arthropod body sizes by 0.2 and 0.5 mm respectively ($z = 2.83$, $P = 0.01$; $z = 6.85$, $P << 0.001$) (Table S6).

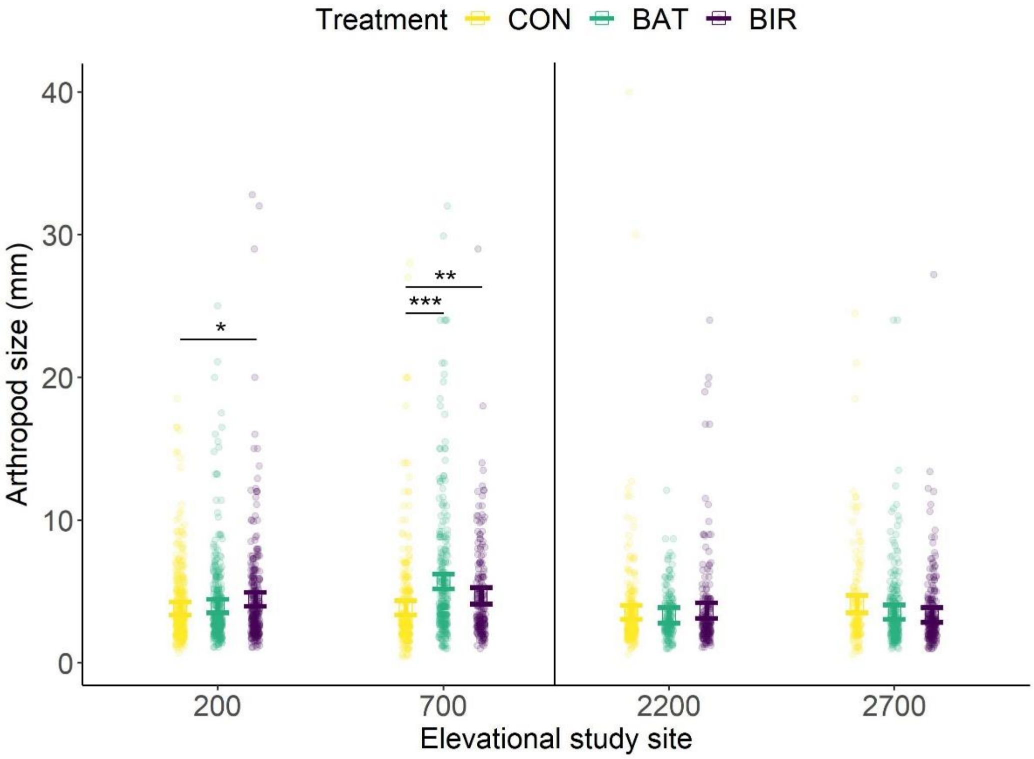

Figure 3. Effect of treatment in interaction with elevation on the size of all arthropods (mm). Estimated marginal means ± confidence intervals are plotted by square and whiskers and means per sample at each elevation are plotted by small dots. Note that we excluded two extreme values (89 and 54 mm) from our dataset. Significantly higher arthropod size in contrast to control, within the elevational study sites, is marked by an asterisk: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. CON = control, BAT = bat exclosure, BIR = bird exclosure.

Herbivory damages

The exclusion of birds and bats led to increased herbivory damage in interaction with elevation ($X_2 = 20.65$, df = 6, $P = 0.002$, Figure 4). At low elevation study sites (i.e., 200 and 700m), despite we observed increases of herbivory damage by 22 and 10% in bat exclosures and by 35 and 43 % in bird exclosures in comparison to control saplings, none of these effects were statistically significant (Figure 4). However, the effect of vertebrate predator exclusion on herbivory damage was revealed to be significant at higher elevations (i.e., 2200 and 2700m).

Bat and bird exclosures significantly increased the herbivory damage by 126 and 82 % at 2200m (z = 3.92, P << 0.001; z = 2.81, P = 0.01, respectively), whereas only bird exclosure significantly increased herbivory by 189 % at 2700m (z = 4.76, P << 0.001). At 2,700m, the effect of bat exclosure was still detectable (i.e., an increase of herbivory by 36 %) but not significant (Figure 4).

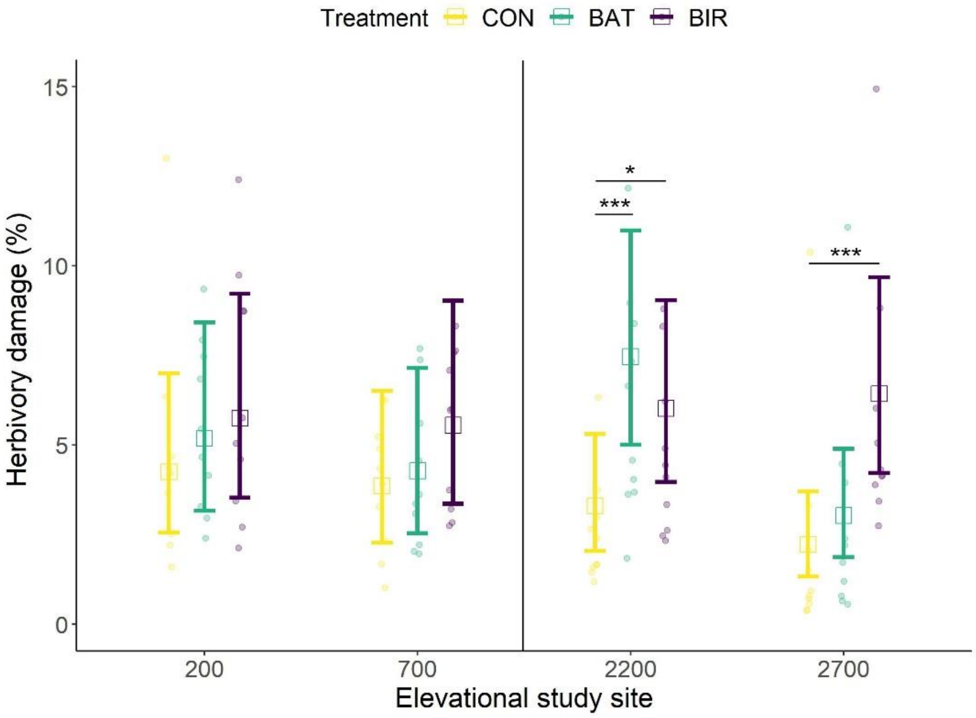

Figure 4. Effect of treatment in interaction with elevation on the herbivory damage (%). Estimated marginal means ± confidence intervals are plotted by square and whiskers and means per sample at each elevation are plotted by small dots. Significantly higher herbivorous damage in contrast to control, within the elevational study sites, is marked by an asterisk: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$. CON = control, BAT = bat exclosure, BIR = bird exclosure.

Discussion

Our study represents the first experiment independently studying the effects of bats and birds on arthropod densities and herbivory damage in undisturbed tropical forests at different elevations. Only birds had a significant effect on arthropod density, particularly on large non-related arthropods, chewers, and mesopredators, regardless of the elevation of the study site. However, these results were not reflected in the herbivory damage. Both birds and bats seemed to limit herbivory only in the highlands. As a result, these findings could highlight potential experimental biases or simply demonstrate the difficulty of establishing a relationship between arthropod densities, herbivory damage and vertebrate predators due to the complexity of tropical rainforest food webs.

Arthropod densities

Contrary to our initial hypothesis, we found that only bird exclosures had a significant effect on the overall arthropod density, regardless of elevation. The 31% increase in arthropod densities observed in the bird exclosures is consistent with another study conducted in a Mexican coffee agroforest (around 30%) during the dry season (Williams-Guillén et al., 2008). The effect of bat exclosures was not significant but detectable, with a 15% increase in arthropod densities. This estimation is similar to those made during the dry season (6%) (Williams-Guillén et al., 2008) but much lower than those made in other tropical regions during the wet season (increase between 84% and 153%) (Kalka et al., 2008; Williams-Guillén et al., 2008). Despite Papua New Guinea has little seasonal variation, slight changes in precipitation and temperature can still negatively impact arthropod densities (Sam et al., 2020) indirectly changing the foraging and feeding behaviours of birds and bats (Jahn et al., 2010; Nurul-Ain et al., 2017), resulting in less pronounced effects of exclosures in the dry season when we conducted the experiment.

Upon closer examination, we found that birds were primarily impacting non-related arthropods (increase in their densities up to 193%), followed by chewer arthropods (by 70%) and mesopredators (by 42%). The observed increase in densities of chewers and mesopredators in bird exclosures supports our second hypothesis and it is consistent with previous findings (Maas et al., 2013; Philpott et al., 2004). However, despite detectable increases in chewer and mesopredator densities in bat exclosures (by 42% and 15%), they were not significant. There were also no notable differences in the effect of bird and bat exclosures on chewer and mesopredator densities among the elevational study sites. As a result, we could not make any conclusions regarding the strength of intraguild predation compared to herbivore suppression across elevations.

In contrast to changes in densities of other arthropods and our expectations, sapsucker densities *decreased* by 87% and 81% in bird and bat exclosures at 700m. This pattern contradicts the results of previous studies in which sapsuckers increased in bat and bird exclosures (Cassano et al., 2016; Maas et al., 2013). Birds and bats may not prefer sapsuckers as prey, due to their small size. The decrease in sapsucker densities therefore likely reflects the observed increase in mesopredator densities in the predator exclosures, which might have been feeding on them.

Nevertheless, the exclosures used in our study likely introduced methodological biases. They did not exclude aerial hawking bats and birds that hunt flying insects present in the surroundings of our experimental saplings. Consequently, this may have attenuated the observed effects of arthropod suppression identified in our experiment, particularly in study sites where hawking bats are most abundant (i.e., at 2,700 meters). In the neotropics, it has been demonstrated that beetles are significant components of the diets of hawking bat species (Rolfe et al., 2014; Salinas-Ramos et al., 2015), as well as adult Lepidoptera (moths) and Diptera (de Oliveira et al., 2020). Since we lack reliable information regarding the dietary preferences of most of the bat species in Papua New Guinea, we can only assume that similar feeding habits may exist in PNG. Additionally, in accordance with Sam et al. (2017), hawking bird species of Papua New Guinea (e.g., *Melanocharis spp.*, *Melipotes sp.*) exhibited a preference for insects from the orders Coleoptera, Hymenoptera, and Diptera. When closely examining the arthropod groups found on our experimental saplings, it is conceivable that the impact of insectivorous birds and bats on arthropod densities may have been underestimated, particularly in the case of some herbivorous orthopterans and beetles (classified as chewers), as well as wasps (classified as mesopredators).

Arthropod sizes

Following our expectations, birds and bats preferred large arthropods, specifically longer than 11 mm, a size that is well above previous estimates (>5 mm) (Philpott et al., 2004; Van Bael et al., 2003). We however observed a difference in the arthropod sizes between elevational study sites when comparing the effect of exclosures. Consistently with Karp and Daily (2014), birds appeared to have a greater impact on larger arthropods particularly at the lowland study sites (200 and 700m). Bats also had a greater impact on larger arthropods at 700m. This is also consistent with previous studies conducted in Mt. Wilhelm, which indicate that larger insectivorous bat and bird species are found more commonly in lowland areas compared to highland regions, likely feeding on larger prey (Sam & Koane, 2020; Sivault et al., 2023).

Even though we did not find large arthropods (maximum 4 cm long) on our control saplings, the mesh size used in our experiment (i.e., 3 cm) could potentially introduce a bias by hindering the movement of larger arthropods to our saplings in the predator exclosures (i.e., the effect we observed might be underestimating the reality). However, only several studies have analysed such biases (Gunnarsson, 2007; Maas et al., 2013; Van Bael et al., 2003). Thus, besides the fact that we ran the experiment during the dry season, this could partially explain why we did not observe significant effects of bird and bat treatment on arthropod densities between elevational study sites.

Herbivory damages

Herbivory damages increased significantly in predator exclosures at 2,200 and 2,700 m, but not in the lowlands. Herbivory increased by 126% at 2,200 m in bat exclosures, while it increased by 82% and 189% at 2,200 and 2,700 m, respectively, in bird exclosures. These values are well above previous estimates, particularly from the dry seasons (0-66%), whether herbivory damage in bat and bird exclosures were examined separately or in combination in other studies (Maas et al., 2013; Sam et al., 2022; Schmitt et al., 2021; Van Bael et al., 2003; Williams-Guillén et al., 2008).

The elevational patterns in the change in herbivory in predator exclosures were in contrast to what has been observed in other parts of Papua New Guinea, where higher herbivory is observed in lowland primary forests (Houska Tahadlova et al., 2023). However, our pattern is consistent with other local exclosure experiments (Sam et al., 2022) and those conducted on other tropical islands (Altmann et al., 2015; Bito et al., 2011; Matías et al., 2015). The impact of the dry season is more pronounced on lowland sites due to insufficient rainfall and elevated temperatures that constrain leaf development. Conversely, highland sites lie beyond the condensation zone, thereby supplying greater moisture to flora and fauna and potentially boosting plant growth and arthropod feeding behaviours.

Furthermore, the higher abundance of insectivorous birds in the highland sites may be associated with the increase in herbivory damage observed in bird exclosures in that region. However, the variations in arthropod densities and the richness and relative abundance of insectivorous bats did not follow the same pattern. Bird species were primarily gleaners across all study sites, while bat gleaners were only found in lowland sites. Nevertheless, it is important to note that many insectivorous bats and birds may specialize in one foraging strategy, but there are instances where they can switch between hawking and gleaning based on factors such as prey type, terrain, and other environmental conditions (Hackett et al., 2014; Ratcliffe &

Dawson, 2003). Therefore, this study highlights the challenge of establishing a clear relationship between trophic levels in such a complex natural tropical system. A future direction for exclosure experiments involves pairing this experimental method with molecular diet analysis (Mata et al., 2021) to determine precisely how individual bat and bird species contribute to the predation/intraguild predation of arthropods and its respective consequences on plants.

Alternatively, we could have unintentionally selected highland experimental plant species, which have weaker direct constitutive defences against herbivore arthropods and rely more on indirect defences via predators (Mrazova et al., 2019). Most past studies have demonstrated that highland plant species tend to have more constitutive defences, as plant biomass is costly in such harsh conditions (Moreira et al., 2018). However, Volf *et al.* (2020) showed that plant species may differ in their investment in defences along the Mt. Wilhelm elevational gradient. This highlights the need to be familiar with the defence strategies of the plant species used in exclosure experiments (i.e., by bottom-up control).

Perspectives

In contrast to our last hypothesis, herbivory damage did not reflect the changes in arthropod densities in predator exclosures across elevations. This highlights the difficulty in establishing a relationship between arthropod densities and herbivory damage. Herbivory accumulates over the entire duration of the experiment, whereas arthropod densities are collected at a given time, and they are likely affected by various factors, such as temperature during collection. Some studies have visually assessed arthropods throughout the study period (weekly or every two weeks) to test for direct effects (Kalka et al., 2008; Morrison & Lindell, 2012; Williams-Guillén et al., 2008). This could be an alternative experimental design to better understand the relationship between herbivory and arthropod predation across elevations. However, this approach would not allow us to test for differences in arthropod sizes between treatments and would reduce accuracy in arthropod identification. Additionally, the leaves used for the herbivory damage analyses were randomly selected at the end of the experiment but not marked at the beginning of the experiment, meaning that the herbivory estimations correspond to standing herbivory compared between the treatments. We thus recommend that for accurate herbivory detection on individual saplings, leaves should be selected and marked before the start of the experiment.

Furthermore, only one study ran exclosures for the same duration as our study (Morrison et al., 2012), while other studies ran exclosures for periods ranging from two months to one year (Cassano et al., 2016; Karp et al., 2014; Vansynghel et al., 2022; Williams-Guillén et al., 2008). A longer experiment may detect different effects of predator exclosures because of seasonal variations affecting predator availability and the life cycle at different levels of the food web, as well as the effect of rare arthropods. We, therefore, recommend taking seasonal patterns in the growth of plants and the activity of arthropods and predators into account in future studies.

Conclusion

This study presents the first bird and bat exclosure experiments in a paleotropical natural system. Our results indicate that birds significantly affect arthropod densities, including leaf chewers and mesopredators, regardless of elevation, while both birds and bats effectively reduce herbivory damage only in the highlands. Due to the complexity of the trophic cascades, we were not able to establish a direct link between arthropod densities, herbivory damage and vertebrate predators. Our study thus provided several recommendations on herbivory measures and arthropod collection for future research. The relationships among trophic levels are intricate and depend on various factors, including the density and types of bird, bat, arthropod, and plant species present, as well as habitat structure and the variation of abiotic factors caused by season and elevation. Given the ongoing global changes, it is expected that bats, birds, and arthropods may need to adjust their distribution along the slopes of Mt. Wilhelm in the coming years. These adjustments will be likely in response to factors like rising temperatures and habitat fragmentation, which have already been observed in other tropical regions (Freeman et al., 2018; Neate-Clegg et al., 2021). As demonstrated in our study, these shifts could have noteworthy implications for herbivory damage on plants. Therefore, it is crucial to better understand how trophic cascades are influenced by these factors, and closely monitor and address the evolving situation.

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Author contributions

BK, LC, and KS conducted the fieldwork, ES performed data analyses and wrote the first draft of the manuscript, KS designed and funded the study and helped with the analyses, and BK, LC and KS contributed significantly to revisions.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Supporting information

Table S1: Number of saplings used per treatment for each of the plant species used in this study according to the elevational study site. CON = control, BAT = bat exclosure, BIR = bird exclosure.

Family	Plant species	Study site											
		200m			700m			2,200m			2,700m		
		CON	BIR	BAT	CON	BIR	BAT	CON	BIR	BAT	CON	BIR	BAT
Phyllanthaceae	*Cleistanthus myrianthus*	2	2	2	7	7	7						
Myristicaceae	*Gymnacranthera paniculate*	3	3	3	2	2	2						
Myrtaceae	*Syzygium thomei*	2	2	2	1	1	1						
Moraceae	*Ficus conocephalifolia*	3	3	3									
Clusiaceae	*Garcinia scretaria*							4	4	4	4	4	4
Lauraceae	*Litsea tomiriana*							2	2	2	4	4	4
Sapotaceae	*Pouteria microphorta*							1	1	1			
Ochnaceae	*Schuurmansia elegans*							1	1	1			
Symplocaceae	*Symplocos cochinchinensis*							1	1	1			
Myrtaceae	*Syzygium benjaminum*							1	1	1	1	1	1
Nothofagaceae	*Nothofagus grandis*										1	1	1

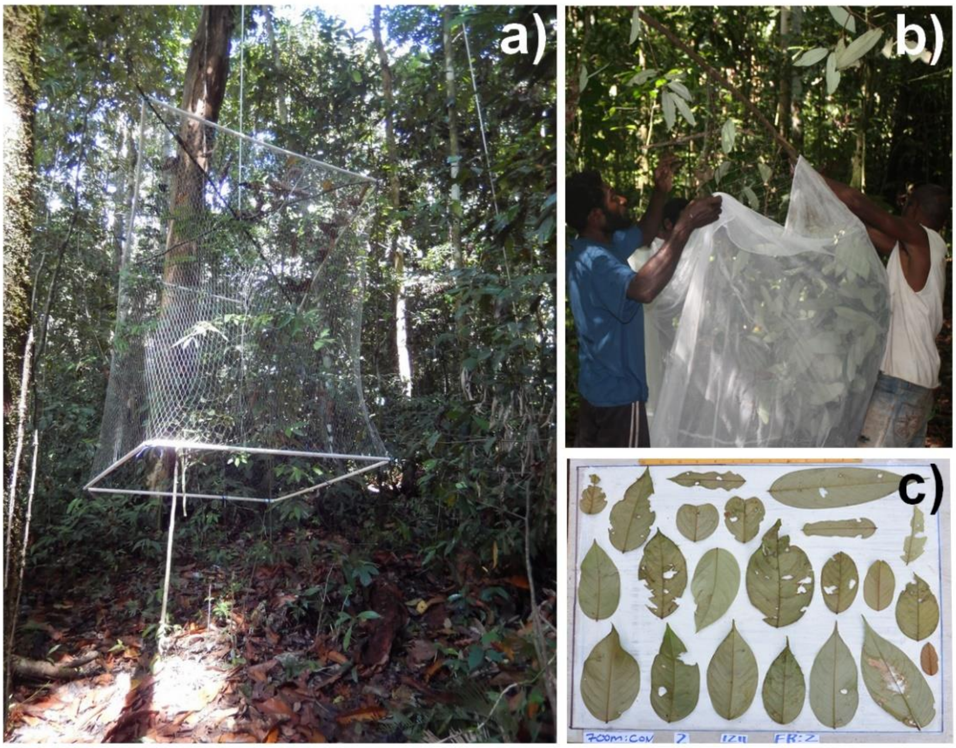

Figure S1: Photos of the study design. Design of the mobile predator exclosures hanging on ropes attached to the canopy trees (photograph by Katerina Sam) (a) collection of the arthropods from the sapling to the large mosquito net (photograph by Katerina Sam) (b) an example of a single leaf frame prepared in the field immediately after leaf collection. The picture shows a random selection of leaves from a single sapling before digital processing (photograph by Lucia Chmurova) (c).

Table S2: Arthropod working groups sorted by feeding guilds following Tahadlova *et al.* (2023) and Sam *et al.* (2022) used in the analysis of this study. The numbers represent the total number of individuals found in the saplings by treatment (all study sites included).

Guild	Working group	CON	BIR	BAT
CHEWERS	Lepidoptera – Larvae	34	57	75
	Phasmatodea	3	2	0
	Gastropoda	4	4	8
	Chrysomelidae	43	36	28
	Curculionidae	42	40	46
	Scarabaeidae	0	0	3
	Coleoptera – Larvae	9	3	0
	Orthoptera	26	61	75
	Attelabidae	0	4	0
	Hymenoptera (wasp – Larvae)	0	0	24
MESOPREDATORS	Araneae	289	288	255
	Formicidae	110	60	125
	Opilionidae	5	11	10
	Staphylinidae	39	31	31
	Coccinellidae	5	7	9
	Chilopoda	2	1	0
	Hymenoptera (wasp – Adult)	37	34	53
	Carabidae	0	2	2
	Malachiidae	9	8	14
	Anthribidae	1	1	2
	Hydrometridae	0	0	1
	Myrmeleontidae	1	0	0
	Anthicidae	1	0	1
	Pseudoscorpiones	0	1	0
	Cantharidae	5	0	0
	Cleroidae	1	0	0
	Pselaphidae	9	2	4
	Scydmaenidae	2	1	1
	Scaphidiinae	0	0	1
	Dermaptera	3	2	2
SAPSUCKERS	Hemiptera – other	139	53	65
	Thysanoptera	1	0	2
NON-RELATED (NR)	Collembola	27	41	40
	Diptera	5	7	4
	Ephemeroptera	2	1	0
	Blattodea	25	14	24
	Lepidoptera – Adult	8	9	14
	Trichoptera	0	1	0
	Acarina	21	5	8
	Amphipoda	0	3	2
	Arhynchobdellida	0	0	1
	Coleoptera – other	34	64	70
	Embioptera	0	0	4
	Apoidae	0	1	0
	Isopoda	5	1	2
	Neuroptera – Adult	1	0	3
	Psocoptera	27	29	33
	Thysanura	1	0	0
	Plathelminthes	3	1	0

Table S3: Relative abundances of the bird species found at the four elevation study sites (i.e., 200m, 700m, 2,200m, 2,700m) including their foraging strategies (i.e., other, gleaner) and feeding guilds (FRIN=Frugivore-insectivore; IN=Insectivore; INFR=Insectivore-Frugivore; INVE=Insectivore-vertebrate; FSIN=Fish-Insectivore; INFL=Insectivore-Flower; INNE=Insectivore-Nectarivore; NEIN= Nectarivore-Insectivore). Bird's preferred diet is in the first position.

Scientific name	**200**	**700**	**2200**	**2700**	**Foraging**	**Guild**
Ailuroedus buccoides	8	1			Other	FRIN
Cicinnurus magnificus		16			Other	FRIN
Edolisoma montanum		2	1	2	Gleaner	FRIN
Henicophaps albifrons		2			Other	FRIN
Melanocharis longicauda				1	Other	FRIN
Melanocharis nigra	21	36	2		Other	FRIN
Melanocharis versteri			38	32	Other	FRIN
Melipotes fumigatus			5	28	Other	FRIN
Pitohui dichrous		18			Gleaner	FRIN
Rhyticeros plicatus	15	31			Other	FRIN
Acanthiza cinerea			4	28	Gleaner	IN
Acanthiza murina			14	3	Gleaner	IN
Aleadryas rufinucha			20	6	Gleaner	INFR
Arses insularis	4	4			Gleaner	IN
Cacomantis castaneiventris		2	2		Gleaner	IN
Cacomantis flabelliformis			7	3	Gleaner	IN
Carterornis chrysomela	11				Gleaner	IN
Centropus menbeki	6				Other	INVE
Ceyx pusillus	1				Gleaner	FSIN
Ceyx solitarus	24	23			Gleaner	INVE
Chrysococcyx ruficollis				1	Gleaner	IN
Colluricincla megarhyncha	14	27	2		Gleaner	IN
Epimachus meyeri				28	Other	INFR
Eugerygone rubra			12	24	Gleaner	IN
Eulacestoma nigropectus				6	Gleaner	IN
Eurystomus orientalis	2				Other	INVE
Gerygone chloronota	6	10			Gleaner	IN
Gerygone chrysogaster	4	26			Gleaner	IN
Gerygone palpebrosa	4				Gleaner	IN
Ifrita kowaldi			2	58	Gleaner	INFR
Machaerirhynchus flaviventer	2	1			Gleaner	IN
Melilestes megarhynchus	16	25	2		Gleaner	INFL
Microeca flavovirescens	9	11			Gleaner	IN
Microeca papuana			25	17	Gleaner	IN

Microptilotis analogus	36	74	1		Gleaner	INFR
Myiagra alecto	11				Gleaner	IN
Pachycephala hyperythra		3			Gleaner	IN
Pachycephala schlegelii			52	87	Gleaner	INFR
Pachycephala simplex		10			Gleaner	IN
Pachycephala soror		13	2	4	Gleaner	IN
Pitohui kirhocephalus	7	52			Gleaner	INFR
Poecilodryas albonotata			2	2	Gleaner	IN
Pomatostomus isidorei	3				Gleaner	INVE
Pseudorectes ferrugineus	16				Gleaner	INFR
Ptiloprora guisei			38	24	Gleaner	INFL
Ptiloprora perstriata			6	54	Gleaner	INFL
Rhipidura albolimbata			64	75	Gleaner	IN
Rhipidura atra			24	28	Gleaner	IN
Rhipidura brachyrhyncha			18	64	Gleaner	IN
Rhipidura hyperythra		4			Gleaner	IN
Rhipidura leucothorax	13	3			Gleaner	IN
Rhipidura rufidorsa		4			Gleaner	IN
Rhipidura rufiventris	7	8			Gleaner	IN
Sericornis nouhuysi			87	60	Gleaner	IN
Sericornis papuensis			13	80	Gleaner	IN
Sericornis perspicillatus			51		Gleaner	IN
Sericornis spilodera		5		1	Gleaner	IN
Syma torotoro	2	11			Gleaner	INVE
Symposiachrus axillaris			6		Gleaner	IN
Symposiachrus guttula	5	1			Gleaner	IN
Symposiachrus manadensis	11	1			Gleaner	IN
Todiramphus macleayii	6	1			Gleaner	INVE
Toxorhamphus novaeguineae	22	45			Gleaner	INNE
Toxorhamphus poliopterus			57		Gleaner	INNE
Tregellasia leucops		1			Gleaner	IN
Xanthotis flaviventer	6	24			Gleaner	INFL
Zosterops minor		20			Gleaner	INFL
Cinnyris jugularis	3				Other	NEIN
Melidectes fuscus				1	Other	NEIN
Myzomela rosenbergii			163	13	Other	NEIN
Philemon meyeri	25	10			Other	NEIN
Pycnopygius ixoides	2	1			Other	NEIN
Zosterops novaeguineae		5	31	2	Other	NEIN

Table S4: Relative activity of bats at the four elevational study sites (i.e., 200m, 700m, 2,200m, 2,700m) including their characteristic call frequencies following Sivault *et al*. (2023). Food preferences and foraging strategies came from Bonaccorso (1998) and the Handbook "The Mammals of the World", vol 9 Bats (Zachos, 2020).

Species	**Call type**	**200**	**700**	**2,200**	**2,700**	**Food**	**Foraging**
HIPPOSIDERIDAE							
Hipposideros wollastoni	*84 mCF*			22		Likely insects	NA
Hipposideros cervinus	*140 sCF*	2				Beetles, moths and other insects	Aerial and gleaning
EMBALLONURIDAE							
Emballonura beccarii / Mosia nigrescens	*62 i.fFM.d*	12	16			Beetles, wingless ants	Aerial and gleaning
Emballonura beccarii / Mosia nigrescens	*72 i.fFM.d*	12					
VESPERTILIONIDAE							
Pipistrellus papuanus	*48 st.cFM*	10				Aerial insects	Hawker
Nyctophilus microtis	*45-50 bFM*	5	4			Insects	Likely aerial and gleaning
MINIOPTERIDAE							
Miniopterus sp. 1 'medium'	*43 st.cFM*	9	11	7	2	Insects	NA
Miniopterus australis [=*Miniopterus* sp. 2 'small']	*54 st.cFM*	5	1		39	Flies, ants, moths, and wasps	Hawker
MOLOSSIDAE							
Austronomus kuboriensis	*13 cFM*		5		3	Beetles	Hawker
Otomops secundus	*18 cFM*				1	Beetles, aerial insects	Hawker

Table S5: Estimated marginal means (=emmeans) of the models including total arthropod density, chewer density, mesopredator density, sapsucker density and NR densities as response variables. Note that the data were standardized prior to the analyses.

Total arthropod densities			
Treatment	emmean	SE	df
CON	-0.21723	0.179619	39.03327
BAT	0.059563	0.179889	38.79783
BIR	0.360771	0.179619	39.03327
Chewer densities			
Treatment	emmean	SE	df
CON	-0.30501	0.176256	38.87119
BAT	0.066374	0.176513	38.60228
BIR	0.315762	0.176256	38.87119
Mesopredator densities			
Treatment	emmean	SE	df
CON	-0.21156	0.181864	35.15484
BAT	0.004985	0.182145	34.99072
BIR	0.372235	0.181864	35.15484
Sapsucker densities			
Treatment	emmean	SE	df
CON-200	-0.01132	0.276051	100.0323
BAT-200	-0.14722	0.278104	88.80716
BIR-200	0.015854	0.276051	100.0323
CON-700	1.809641	0.296608	48.46158
BAT-700	-0.33747	0.296608	48.46158
BIR-700	-0.1744	0.296608	48.46158
CON-2200	-0.25593	0.281202	108.4042
BAT-2200	-0.36465	0.281202	108.4042
BIR-2200	-0.12004	0.281202	108.4042
CON-2700	-0.33747	0.28424	82.67853
BAT-2700	-0.01132	0.28424	82.67853
BIR-2700	-0.06568	0.28424	82.67853
NR densities			
Treatment	emmean	SE	df
CON-200	-0.3884	0.21282	35.654
BAT-200	-0.2789	0.213416	33.78939
BIR-200	0.136642	0.21282	35.654
CON-700	-0.60553	0.2421	9.587015
BAT-700	-0.49603	0.242028	9.749017
BIR-700	-0.08049	0.2421	9.587015
CON-2200	0.165655	0.22088	42.07087
BAT-2200	0.275155	0.220909	41.95745
BIR-2200	0.690696	0.22088	42.07087

CON-2700	-0.01778	0.22388	23.29987
BAT-2700	0.091718	0.223909	23.24817
BIR-2700	0.507259	0.22388	23.29987

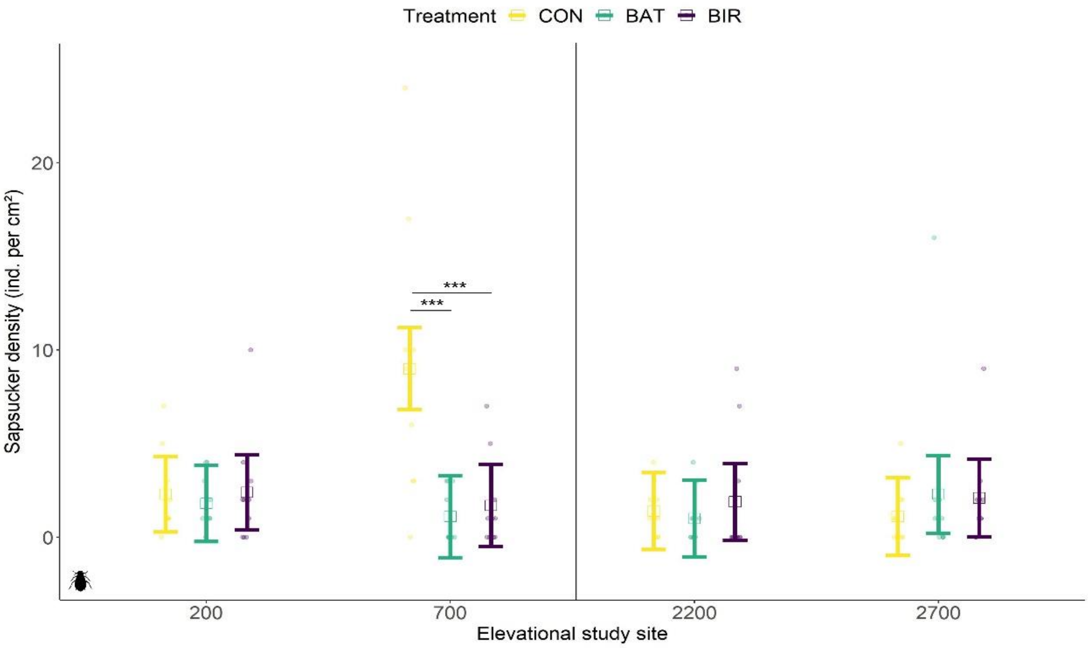

Figure S2: Effect of treatment on the sapsucker density per sample summarized between elevational study sites separately. Estimated marginal means ± confidence intervals are plotted by square and whiskers, means per sample at each elevation are plotted by small dots. CON = control, BAT = bat exclosure, BIR = bird exclosure, significance is marked as follow: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, NS $P > 0.05$.

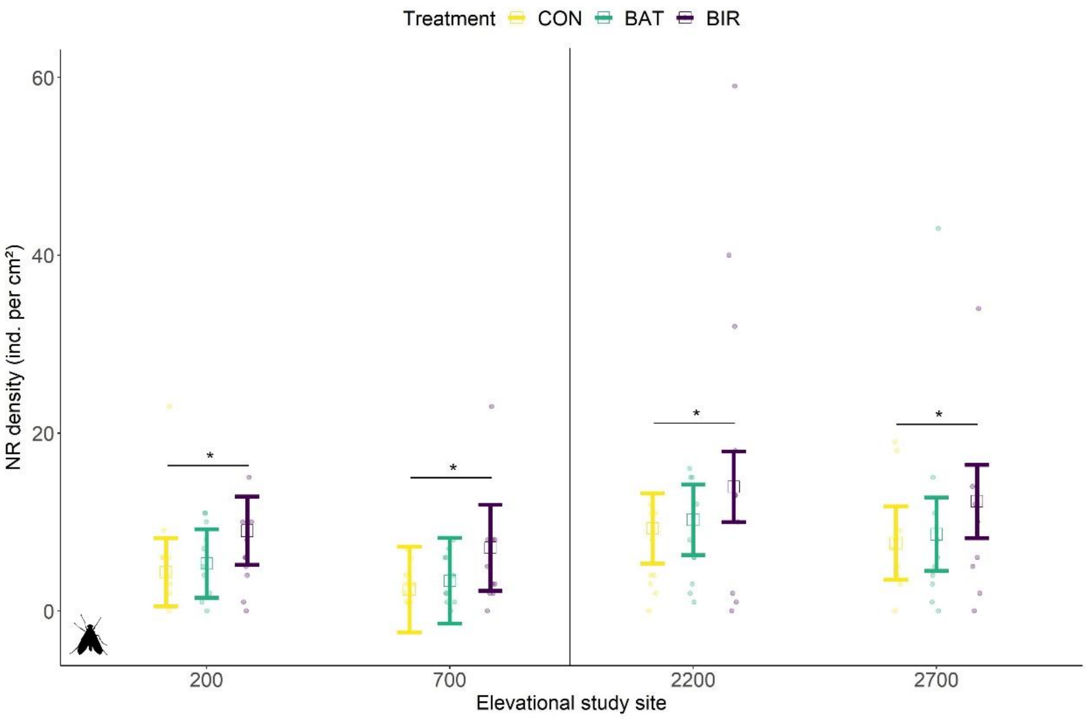

Figure S3: Effect of treatment on the NR (non-related arthropods) density per sample summarized between elevational study sites separately. Estimated marginal means ± confidence intervals are plotted by square and whiskers and means per sample at each elevation are plotted by small dots. Note that the results came from an additive model. CON = control, BAT = bat exclosure, BIR = bird exclosure, significance is marked as follow: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, NS $P > 0.05$.

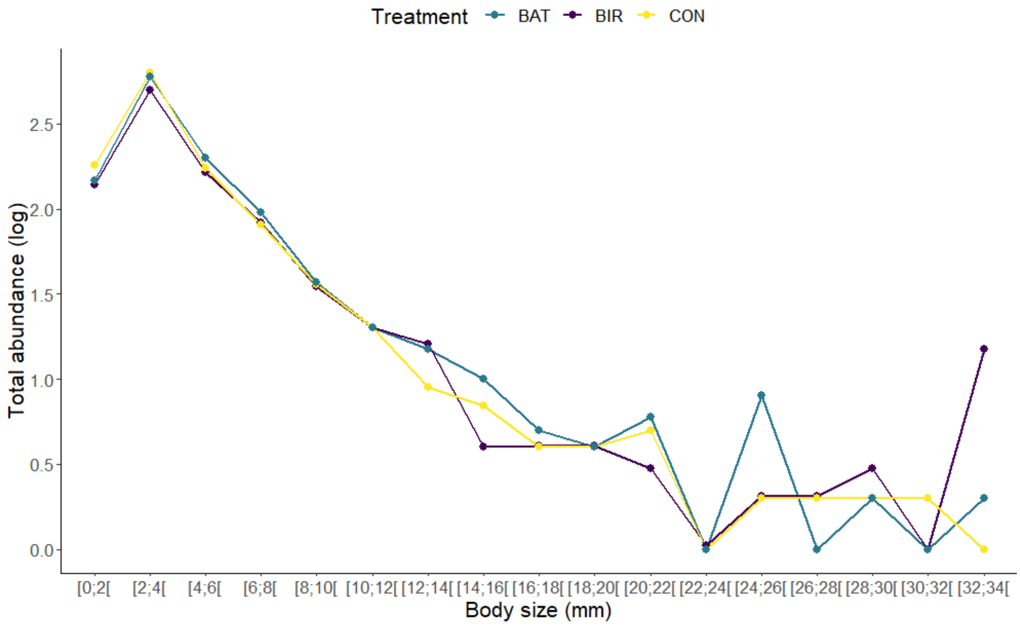

Figure S4: Total abundance of arthropods (log) per body size class of 2 mm per treatment. Note that extreme values above 32 mm were removed from this plot. CON = control, BAT = bat exclosure, BIR = bird exclosure.

Table S6: Estimated marginal means (=emmeans) of the models including arthropod sizes and herbivory damage as response variables. Note that the data were standardized prior to the analyses.

Arthropod sizes			
Treatment	emmean	SE	df
CON-200	-0.06742	0.057909	32.66583
BAT-200	-0.02454	0.060264	36.0929
BIR-200	0.10206	0.062904	47.48878
CON-700	-0.05531	0.066151	49.81505
BAT-700	0.430669	0.068229	52.87424
BIR-700	0.166041	0.075876	83.36495
CON-2200	-0.14096	0.064418	85.44174
BAT-2200	-0.19533	0.073249	156.645
BIR-2200	-0.10892	0.07221	135.6242
CON-2700	0.014643	0.08154	186.6362
BAT-2700	-0.13454	0.066289	75.34506
BIR-2700	-0.18854	0.069125	90.32404
Herbivory damage			
Treatment	response	SE	df
CON-200	0.04253	0.010828	106
BAT-200	0.051907	0.012869	106
BIR-200	0.057433	0.013959	106
CON-700	0.038611	0.010278	106
BAT-700	0.042776	0.01124	106
BIR-700	0.05548	0.013869	106
CON-2200	0.033026	0.007966	106
BAT-2200	0.074635	0.014795	106
BIR-2200	0.060208	0.012522	106
CON-2700	0.022235	0.00577	106
BAT-2700	0.030336	0.007364	106
BIR-2700	0.064232	0.013489	106

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Chapter 4

Insectivorous birds and bats outperform ants in the top-down regulation of arthropods across strata of a Japanese temperate forest

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Insectivorous birds and bats outperform ants in the top-down regulation of arthropods across strata of a Japanese temperate forest

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Abstract

1. Birds, bats, and ants are recognized as significant arthropod predators. However, empirical studies reveal inconsistent trends in their relative roles in top-down control across strata. Here, we describe the differences between forest strata in the separate effects of birds, bats, and ants on arthropod densities and their cascading effects on plant damage.

2. We implemented a factorial design to exclude vertebrates and ants in both the canopy and understory. Additionally, we separately excluded birds and bats from the understory using diurnal and nocturnal exclosures. At the end of the experiments, we collected all arthropods and assessed herbivory damage.

3. Arthropods responded similarly to predator exclusion across forest strata, with a density increase of 81% on trees without vertebrates and 53% without both vertebrates and ants. Additionally, bird exclusion alone led to an 89% increase in arthropod density, while bat exclusion resulted in a 63% increase. Herbivory increased by 42% when vertebrates were excluded and by 35% when both vertebrates and ants were excluded. Bird exclusion alone increased herbivory damage by 28%, while the exclusion of bats showed a detectable but non-significant increase (by 22%). In contrast, ant exclusion had no significant effect on arthropod density or herbivory damage across strata.

4. Our results reveal that the effects of birds and bats on arthropod density and herbivory damage are similar between the forest canopy and understory in this temperate forest. In addition, ants were not found to be significant predators in our system. Furthermore, birds, bats, and ants appeared to exhibit antagonistic relationships in influencing arthropod density. These findings highlight, unprecedentedly, the equal importance of birds and bats in maintaining ecological balance across different strata of a temperate forest.

Introduction

Arthropod herbivores play a critical role as primary consumers of leaf tissue in forest ecosystems (Coley, 1991; Coley & Barone, 1996). This may have various effects not only on individual plants but also on vegetation as a whole, such as plant growth and fitness (Garcia & Eubanks, 2019), species composition (Bagchi et al., 2014), and nutrient cycling (Belovsky & Slade, 2000; Chapman et al., 2003).

By feeding on arthropod herbivores, insectivorous predators indirectly increase plant biomass, creating what is commonly known as top-down control or a trophic cascade (Paine, 1966, 1980). However, the strength of top-down control by insectivorous predators varies due to factors such as prey availability (Garrett et al., 2022), predation rate (i.e., the consumption of prey by predators per unit of time; Thomine et al., 2020), and the magnitude of non-consumptive effects (i.e., alterations in prey behaviour in the presence of predators; Kollross et al., 2023). Given the complexity of food webs, the degree of top-down control is context-dependent, leading to variations even within a single forest and among different forest strata. Unfortunately, research on trophic cascades has so far predominantly focused on easily accessible forest understories (Denmead et al., 2017; Ocampo-Ariza et al., 2023), limiting our understanding of their full extent (e.g., forest canopy).

The impact of different predator groups on arthropod densities can vary, and when their effects overlap, it can become challenging to distinguish the individual contributions of each predator group (Mooney, 2007; Perfecto & Vandermeer, 1996; Richards & Coley, 2007; Sih et al., 1998). An obvious step to evaluating trophic cascades is thus to observe what happens when the abundance or community composition of predators is altered. To address this, a common experimental approach is the use of exclosure experiments (Maas et al., 2019), which exclude different predator groups from insect prey and foliage.

Vertebrate insectivores, such as birds and bats, are the most well-known top predators of terrestrial arthropods (Böhm et al., 2011; Johnson et al., 2010; Karp & Daily, 2014; Maas et al., 2013; Mooney et al., 2010; Nyffeler et al., 2018). Previous research, employing diurnal and nocturnal exclusions to differentiate the individual contributions of birds and bats, has generally emphasized significant impacts on arthropod communities attributed to bats alone (Cassano et al., 2016), birds alone (Gras et al., 2016), or both (Williams-Guillén et al., 2008; Kalka et al., 2008; Ocampo-Ariza et al., 2023; Maas et al., 2013; Morrison & Lindell, 2012). Nevertheless, most of these studies were conducted in the tropics, leaving the individual contributions of insectivorous birds and bats to top-down control still poorly understood in temperate regions.

In addition to vertebrate insectivores, certain groups of arthropod insectivores, particularly ants, are also expected to have a significant role in trophic cascades. Although they have been extensively studied as natural enemies and biological control agents (Mestre et al., 2012; Philpott & Armbrecht, 2006; Rosumek et al., 2009; Schifani et al., 2020; Tobing & Kuswardani, 2018), their importance as key predators remains uncertain both in tropical and temperate forests (Pérez-Espona, 2021; Sanders & van Veen, 2011; Thurman et al., 2019) . This uncertainty persists because only a limited number of studies (Gras et al., 2016; Vansynghel et al., 2022; Ocampo-Ariza et al., 2023) have aimed to exclude ants while also considering vertebrate predators. Within this limited scope, findings have been mixed, with studies showing both negative (Denmead et al., 2017; Singer et al., 2017) and positive (Ocampo-Ariza et al., 2023) effects of ants on the abundance of mesopredators and herbivorous arthropods.

The combined predatory activity of multiple groups may have additive (Morrison & Lindell, 2012; Williams-Guillén et al., 2008), synergistic (Losey & Denno, 1998) or even antagonistic effects (Ferguson & Stiling, 1996; Mooney, 2007) on the control of arthropods. Compared to ants, insectivorous birds and bats primarily target larger arthropods (Philpott et al., 2004; Van Bael et al., 2003), and their diurnal and nocturnal foraging behaviour gives them access to distinct prey types. In such instances, their combined impact on arthropod communities equals the sum of the arthropods consumed by each group independently (i.e., additive effect). Although that is the logic, some studies failed to demonstrate this additive effect between birds and bats (Maas et al., 2013) or among birds, bats, and ants (Vansynghel et al., 2022). Nevertheless, acknowledging the distinct dietary preferences observed among ants, birds, and bats, we expect that they will evenly and strongly affect arthropod densities and that their effects will be additive **[H1]**.

It remains unclear whether, or under which conditions, predators indirectly affect plants (Mooney et al., 2010). This uncertainty emerges because predators can also function as intraguild predators, consuming predatory arthropods. When predators simultaneously consume predatory arthropods and herbivores, their net effect on plants could be dependent on the balance between these two factors. Research indicates that the impact of the exclusion of vertebrates and ants on plants may be moderately counterbalanced by the release of spiders, carabid beetles, and other predatory arthropods (Williams-Guillén et al., 2008; Maas et al., 2013) or through mutualism with sap-sucking herbivores (i.e., aphids and mealybugs) harmful to plants (Gras et al., 2016; Wielgoss et al., 2012; Ocampo-Ariza et al., 2023). Yet, numerous studies have demonstrated that the absence of predators can lead to significant cascading effects on plants, even in the presence of intraguild predation (Cassano et al., 2016; Gras et al., 2016; Bouarakia et al., 2023; Kalka et al., 2008; Morrison & Lindell, 2012; Ocampo-Ariza et al., 2023). We can thus expect that birds, bats, and ants, despite being intraguild predators and/or mutualists with plant-sucking insects, will indirectly diminish herbivory damage **[H2]**.

Forest canopies are crucial for the overall functioning of forest ecosystems (Ozanne et al., 2003). According to ecological theories, species interactions are more intense and species richness is higher in the warmer and more productive forest canopies than in the cooler understories (Basset et al., 2015; Janzen, 1970; Nakamura et al., 2017; Schemske et al., 2009).

However, this is not always consistent with empirical findings. Various studies have reported an opposite or variable pattern of abundance and diversity of different arthropod taxa across tropical, subtropical, and even temperate forest canopies (Aikens et al., 2013; Basset et al., 2003; Compton et al., 2000; De Dijn, 2003; De Vries, 1988; DeVries et al., 1997; Haack et al., 2022; Hill et al., 1992; Intachat & Holloway, 2000; Larrivée & Buddle, 2009; Schulze et al., 2001; Ulyshen, 2011). Moreover, the effects of predators on plants through trophic cascades have seldom been investigated across the strata of temperate forests (Aikens et al., 2013; Böhm et al., 2011).

According to the optimal foraging theory, predators should allocate more time to foraging in areas with higher prey density to reduce search time (Balza et al., 2020; Emlen, 1966; MacArthur & Pianka, 1966; Piel et al., 2021). Additionally, most birds in temperate forests are expected to be foraging strata generalists (Marra & Remsen Jr, 1997). Similarly, in the northern hemisphere, there is no clear stratification of bat species composition between the canopy and understory (Collins & Jones, 2009; Kalcounis et al., 1999; Plank et al., 2012; Zeus et al., 2017). In contrast, understory dominance is more pronounced among ants in temperate forests (Seifert, 2008). In light of these observations, we predict that the impact of ants on arthropods, and indirectly on herbivory, will be more pronounced in the forest understory and anticipate that the impact of vertebrate predators will be most prominent in strata with higher arthropod densities (which vary between canopy and understory across studies), according to the optimal foraging theory **[H3]**.

To address the aforementioned hypotheses, we individually excluded birds, bats and ants in a fully factorial design that allowed us to separate the effects of predators on the arthropod densities in the understory and canopy of a temperate forest in Japan. We complemented our research on the impact of predators on arthropods and plants by conducting surveys of the excluded predator communities.

Materials and Methods

Study site

We conducted our experiment in the Tomakomai experimental forest in Japan (42° 40 '48.0"N 141° 35' 24.0 "E, 50m a.s.l.). The study area covers a total of 2,720 hectares of low elevation terrain (elevation range: 20-90 m a.s.l.) and has canopy crane access (Figure S1.1 in Appendix S1). It is situated on a hillside within the district, approximately 4 kilometres from the Pacific Ocean. The forest belongs to a cool, temperate zone and is composed of approximately 25% artificially planted conifers (e.g., *Picea glehnii* and *Abies sachalinensis*) and 75% young secondary deciduous forest, mainly occupied by broad-leaf trees dominated by oak (*Quercus crispula*), ash (*Fraxinus lanuginosa*), maple (*Acer mono, A. palmatum*) and elm (*Ulmus davidiana*), regenerated after typhoon damage (Wu et al., 2019). The temperature ranges from -22°C to 28 °C depending on seasonality. Annual precipitation ranges between 800 to 1,600 mm.

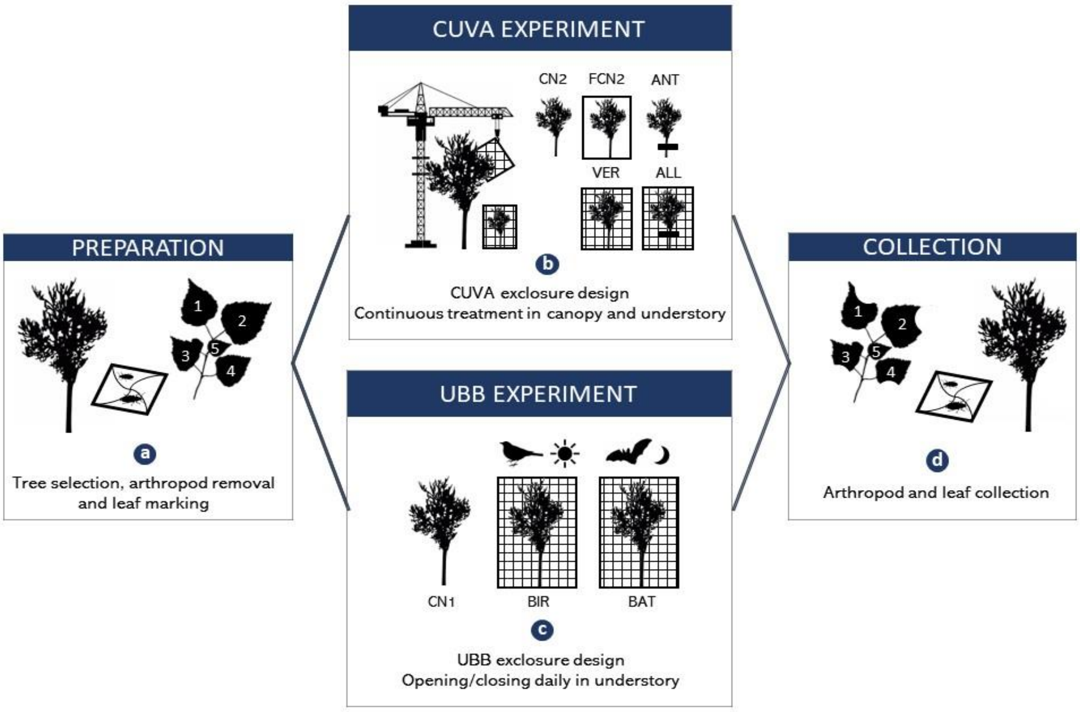

Figure 1. Schematic design of the experimental setup used in the study: (a) Pre-selection of individuals, removal of arthropods and assessment of preexisting herbivory on developing

leaves to establish a baseline for the experiment; (b) Canopy - Understory Vertebrate and Ant exclusion (CUVA) experiment setup performed on branches in the canopy and on saplings in the understory; (c) Understory Bird and Bat exclusion (UBB) experiment, performed only on saplings in the understory; (d) Final arthropod collection and leaf herbivory survey at the end of each experiment. CN1 and CN2 = control treatments, FCN2 = frame-control treatment, ANT = ant exclosure, VER = exclosure of vertebrate predators, ALL = exclosure of vertebrates and ants, BIR - bird exclosure, BAT = bat exclosure.

Treatment preparation

We preselected eight plant species in the understory and seven in the canopy (Table S1.1) based on their abundance in the forest understory and canopy, and accessibility from the crane (Figure 1a). For each plant species, we identified suitable individuals - "saplings" (i.e., young trees, 1.5-3 m tall) in the understory and canopy "branches" (i.e., 1-1.5 m long branches of adult trees). The branches in the canopy had a comparable size and number of leaves to the saplings in the understory. Trees used for the canopy experiment extended to heights ranging from 12 to 22 metres (Matsuo et al., 2022), resulting in a vertical separation of approximately 10.5 to 20.5 metres between the canopy and the understory.

We carried out two distinct experiments, each was conducted twice; first in 2018 and then replicated in 2019, using a distinct set of individuals each year. A total of 120 saplings were used each year for the Understory Bird and Bat exclusion (UBB) experiment (Table S1.3), which was conducted exclusively in the understory. For the Canopy - Understory Vertebrate and Ant exclusion (CUVA) experiment, we used 84 branches and 160 saplings each year (Table S1.2).

To establish a baseline at the beginning of the experiment, we removed all arthropods from the understory saplings and canopy branches by shaking the foliage repeatedly. Additionally, we manually inspected the leaves to remove any remaining arthropods.

To assess herbivory damage at the end of the experiment, once the first leaves were fully developed, we randomly selected three small twigs from each sapling, ensuring they had at least ten leaves and showed no signs of herbivory. Each twig was marked and had ten leaves numbered individually with a permanent marker. Then, we randomly assigned the individuals to a given experiment (UBB or CUVA) and a treatment.

Canopy - understory vertebrate and ant exclusion (CUVA)

To determine the strata and predators that induce stronger trophic cascades and to test for the additivity of vertebrate and ant effects, we initially conducted the CUVA experiment. The experiment was conducted in both the canopy and understory (Figure S1.1), between May and July 2018 and 2019 (Table S1.4), until the end of the growing season which was determined by the leaf fall of *Prunus* species. The experiment lasted 65 ± 3 days. The experimental design consisted of setting up exclosures of vertebrates (VER), ants (ANT), and all predators combined (ALL). Each treatment was matched with a CUVA experiment control treatment (CN2), and a frame-control treatment (FCN2, Figure 1b). Each treatment was set on five individual saplings in the understory and three branches in the canopy for each of the eight/seven plant species in each year of collection (Table S1.2).

We constructed vertebrate exclosures (VER) using bamboo poles covered with agricultural transparent green netting, with a mesh size of 3 x 3 cm, which was comparable to mesh sizes used in other exclosure studies (e.g., Greenberg: 29×29 mm, Greenberg et al. 2000; Mols and Visser: 25×25 mm, Mols & Visser 2002; Van Bael: 20×20 mm, Van Bael et al. 2003). Each exclosure measured 2 x 2 x 2.5 m and had a total volume of 10 m3 in the understory, while in the canopy, they measured 1.5 x 1.5 x 1.5 m with a volume of 3.38 m3, enclosing an average of 1.63 m2 (± S.E. 0.06) of leaf area. The vertebrate exclosures were set permanently for the whole duration of the experiment in each year. The nets made firm contact with the ground in the lower part of the exclosures (Figure S1.2), and we securely fastened them to branches for canopy branches. Our observations confirmed that small insectivorous lizards and terrestrial mammals could access the exclosures, although we rarely observed them. We took special care to ensure that the foliage of the inner sapling did not touch the netting or cage construction, preventing flying vertebrates from accessing arthropods through the mesh. Importantly, the exclosure materials neither attracted arthropods nor caused damage to leaves or branches, and they did not reduce light exposure.

Ants (ANT) were excluded using a Tanglefoot sticky pest barrier (Philpott et al., 2004; Philpott et al., 2008). We applied the adhesive in a 10-15 cm wide stripe around the entire circumference at either the breast height of sapling trunks or the thickest section of canopy branches. Additionally, we removed all tall herbs and foliage in the surrounding area that could act as vegetation bridges, so the individual tree would not become accessible to ants after the treatment was set up.

To exclude all predators (ALL) we used a combination of the aforementioned methodology to exclude vertebrates and ants. Additionally, tangle glue was applied along any supportive ropes attached to the cage that could be used as a bridge for foraging ants.

The controls (CN2) were not enclosed by any constructions or protected by a tanglefoot barrier. The frame-controls (FCN2), on the other hand, were surrounded by identical bamboo constructions with dimensions 2 x 2 x 2.5 m (Figure S1.2). However, we did not surround these structures with agricultural nets. We used this treatment to investigate whether the construction had any unintended effects on the experiment, such as deterring vertebrate predators or attracting more mesopredators.

Understory bird and bat exclusion (UBB)

To assess the additivity of bird and bat effects (H1), we subsequently conducted the UBB experiment. The experiment was conducted between May and June in 2018 and 2019 (i.e., the whole experiment was replicated twice) (Table S1.4). The exclosure experiment always lasted 30 ± 2 days. We set up exclosures for birds (BIR) and bats (BAT) with additional UBB experiment control saplings (CN1) (Figure 1c). Each of the three treatments was set on five individual saplings per plant species each year (Table S1.3). We exclusively conducted this experiment in the understory.

To exclude birds (BIR) or bats (BAT) separately, we used similar exclosure cages to those used for the VER treatments (Figure S1.2). The netting was pulled up to allow predators to access the sapling and down to exclude them. We moved the netting up or down ±30 min around sunrise and ± 30 min around sunset, ca. 4:15 AM and ca. 6:40 PM in mid-May, respectively, adjusted to the real sunrise and sunset daily. For BIR exclosures, we opened the exclosures during the night and closed them during the day and vice versa for BAT. As for CN2, individuals in CN1 were only marked.

Collection of the experiments

The leaves marked at the beginning of the experiments were collected at the end of the experiments (Figure 1d). Individual leaves were scanned (EPSON, 600 dpi, colourful tiff format) within 12 hours of collection (Figure S1.2). To analyse insect herbivory, we first outlined any missing parts of leaves in Photoshop® using the protocol established by Sam et al. (2020). Then, we calculated the remaining area (a) and the full expected area of each leaf (b), in cm^2 using ImageJ version 1.47 (National Institute of Health, USA) in order to calculate the total area eaten by herbivores (c), ($c = b - a$) per leaf. We then calculated the proportion of leaf area loss as c/b. To determine the total leaf area of each individual sapling or branch, we calculated the mean leaf area based on the leaves collected for herbivory assessment. Then we multiplied it by the total leaf count in each sapling or branch using the mean value obtained from three independent estimations conducted by sampling technicians.

To survey the effect of our treatments at the end of each experiment, we first accessed the individuals and cut open the cages where needed. We lowered the crown of the individuals above a 1.5 x 1.5 m beating sheet (i.e., we had full access to the branches thanks to the canopy crane), shook the foliage vigorously five times and quickly captured all arthropods that had fallen on the sheet (Figure S1.2). We then inspected the leaves for any concealed arthropods and took notes on any arthropods that escaped during the beating process. We added these observations later to the dataset. We stored the arthropods in vials filled with DNA grade 95% ethanol solution. All individual arthropods were later categorised into morpho-species, measured, and identified into their taxonomic order in the laboratory in the Czech Republic. Individuals were then assigned to one of four feeding guilds: predator, leaf chewer, sapsucker, or no relationship (i.e., arthropod with no consumptive effect on other arthropods or plants, NR). The developmental stage of the arthropods was taken into account when assigning them to feeding guilds. For instance, adult Lepidoptera were classified as having "no relationship," while their caterpillars were categorised as "chewers". To calculate arthropod density, the number of arthropod individuals was determined per square metre of total leaf area of the individual sapling or branch. Closer identifications were done where needed to assign each individual to a given feeding guild.

Predator survey

We used baits to survey both terrestrial (those that nest or forage on or in the leaf litter) and arboreal (those that forage or nest in the canopy) ants. The baits were exposed on eight randomly selected tree individuals of each of the eight focal plant species (i.e., 64 saplings in the understory and 64 branches in the canopy) during the second year of collection (i.e., 2019). We selected trees and branches different from those used in the exclosure experiment for the ant survey to avoid the disturbance of the experiment. Yet, the trees used for the ant survey were growing in the same plot but randomly scattered among the individuals used for the exclosures and were of a similar size and amount of foliage. Two types of baits (each roughly 2-3 cm^3) were used: 1) tuna chunks in vegetable oil (Giana®) and 2) cotton balls soaked in sugar paste and wrapped in a piece of gauze. Baits were set out at each selected sapling or canopy branch, attached with a string, and separated by at least 20 cm, and an alternating position of the bait was used (i.e., lower or higher on the trunk of saplings, and either closer or further from the trunk on canopy branches, or altering positions on a fork-shaped branch if available). We checked the baits after 4 hours of exposure and visually morphotyped and counted any ants feeding on them. Up to five individuals of each morphotype crawling on the bait were collected and put into 2 ml vials filled with DNA-grade ethanol (99%). During sampling, information about the time, weather conditions, bait position, ant morphotype and the abundance per morphotype was recorded on datasheets. We later identified ants in the laboratory using the species level key (Ichinose, 1990; Imai et al., 2003) based on records of existing ant species at the study site (Ichinose, 1990). While collecting the baits, the surrounding branches were examined for additional ants that may have been feeding on the baits prior to inspection.

We used point counts and Song Meter recordings to assess bird communities during the second year of collection (i.e., 2019). Point counts were carried out at 16 points regularly spaced along a 2,350-m transect at the study site; successive points were 150 ± 5 m apart to avoid overlap. All birds seen or heard within a fixed radius of 0–50 m (estimated or measured by a laser rangefinder) were recorded, and the height of the individual above ground was noted. We started surveys 15 minutes before sunrise, each count lasted 15 minutes. This ensured that all 16 points were surveyed before 11:00 AM (Sam et al., 2019). All points were surveyed equally, and the survey (i.e., all 16 points represents one replication in time) was replicated fifteen times (i.e., in 15 days). A Song Meter SM3BAT (Wildlife Acoustics Inc.) with one external acoustic (SMM_A1, Wildlife Acoustic) and one ultrasonic (SMM_U1, Wildlife Acoustic) microphone was set to record the first 10 minutes of every 30 minutes (10 min recording, 20 min sleeping) from 3:00 AM to 9:00 PM. The Song Meter was set up for 15 days in the forest canopy (17m above the ground) during the first month of the experiment and for 15 days in the forest understory (1.5m above the ground) during the second month of the first year of collection (i.e., 2018). We used manual identification of the bird calls from the recordings and determined species richness and relative abundances of birds in the understory and canopy.

Similarly, we estimated bat communities using the same Song Meter. The Song Meter was set for 14 days in the forest canopy and 14 days in the forest understory during the second year of collection (i.e., 2019) using the same parameters as the bird survey. The recordings were divided into five-second files and analysed by opening each WAV file in Kaleidoscope Pro Software (Wildlife Acoustics Inc.) and manually inspecting the spectrograms for bat echolocation pulses. The sampling rate was 192 kHz which is above the range of frequencies emitted by the bats in this area (20-86 kHz) (Fukui et al., 2004). Echolocation call types were recognised from the recordings and attributed to a bat species (when possible) based on literature (Fukui et al., 2004). We measured bat activity from the Song Meter recordings as a proxy of abundance. We defined a ‘bat pass’ as a sequence with at least two recognisable echolocation pulses per species emitted by a flying bat within a 5-second sound file (Kerbiriou et al., 2019). Bat activity was quantified as the number of bat passes recorded for each species. Later on, we used the Handbook of the Mammals of the World (Zachos, 2020) and Handbook of the Birds of the World (Del Hoyo et al., 1996) to obtain the body weight and feeding guild of each bird or bat species to determine the biomass of insectivorous predators at each forest strata.

Statistical analysis

We built linear mixed-effect models using the package "lme4" (Bates et al., 2015), to test the effect of treatment (factor of 4 levels: CN2, VER, ALL, ANT), strata (factor of 2 levels: canopy and understory) and their interaction on log-transformed total arthropod densities (number of individuals per cm^2 of foliage) and arthropod densities partitioned into four feeding guilds: chewers, mesopredators, sapsuckers and no relationship (hereafter referred to as NR) for the CUVA experiment. All the models additionally contained the sampling year (factor of 2 levels) as a fixed effect and individual trees (factors of 361 levels) and plant species (factor of 8 levels) as random effects. We also considered strata both as a fixed effect and as a random slope for the plant species (referred to as Plant species: Strata in Table S2.1) to account for species differences between strata.

Then, we ran generalised linear mixed-effect models using the package 'glmmTMB' (Brooks et al., 2017), using a beta error distribution and the same predictors as above to model herbivory damage (the proportion of the leaf area lost per branch). All the models contained the sampling year as a fixed effect and individual trees, branches (factor of 487 levels) and plant species as random effects. We again considered strata both as a fixed effect and as a random slope for the plant species. To select the best models, we built models with all possible combinations and used the AICctab function from the 'bbmle' package (Bolker & Bolker, 2017), which computes the corrected Akaike information criterion of all our models (Table S2.1, S2.2). For each best model, we obtained estimated marginal means (= emmeans) and pairwise comparisons (Tukey Post Hoc) among all variable levels (Table S2.3, S2.4, S2.5, S2.6, S2.7), using the 'emmeans' package (Lenth, 2018). We controlled the model's quality and fit with the 'performance' package (Lüdecke et al., 2021).

We then constructed linear mixed-effect models to test the effect of treatment (factor of 3 levels: CN1, BAT, BIR) on log-transformed total arthropod densities and arthropod densities partitioned in four feeding guilds: chewers, predators, sapsuckers and NR for the UBB experiment. All the models contained the sampling year as a fixed effect and plant species (factor of 8 levels) as a random effect. Then, generalised linear mixed-effect models using a beta error distribution were used to determine the effect of treatment on herbivory damage. All the models contained the sampling year as a fixed effect and plant species and individual trees (factor of 240 levels) as random effects. The best models were selected following the same method as for the CUVA experiment (Table S2.8, S2.9), as well as for their estimated marginal means (Table S2.10).

To provide context, we used Wilcoxon rank sum tests to compare total arthropod densities, predator, chewer, sapsucker and NR densities, and herbivory between the canopy and understory control treatments (CN2). To investigate whether the construction had any unintended effects on the experiment, we also used these tests to compare total arthropod and mesopredator densities between control (CN2) and frame-control (FCN2) in the understory. All analyses were performed using R Statistical Software (v4.3.1; R Core Team, 2020).

Results

Arthropod density and herbivory damage after the CUVA experiment

In total, we collected 10,649 arthropods from 488 individual branches and saplings across 9 plant species (i.e., two years combined). We found that the overall arthropod densities, as well as predatory arthropod densities, on control individuals, were significantly lower in the canopy than in the understory ($W = 2245$, $P = 0.002$ and $W = 2539$, $P < 0.001$) (Figure S3.1), whereas the arthropod chewer, sapsucker and NR densities on controls did not vary significantly between forest strata (see Table 1 for more details).

Table 1: Mean arthropod density per square metre (i.e., total and split into feeding guilds) and herbivory damage (%) found in the control individuals in the canopy and understory (± standard

error). Significant comparisons between the canopy and understory are marked as follows: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

Strata	Total arthropods **	Chewers	Predators ***	Sapsuckers	NR	Herbivory (%) ***
Canopy	22.2 ± 3.9	2.8 ± 0.5	5.0 ± 1.0	2.9 ± 0.6	11.4 ± 3.2	5.1 ± 0.5
Understory	46.1 ± 6.0	13.2 ± 3.9	24.3 ± 4.3	1.9 ± 0.5	6.6 ± 1.4	8.5 ± 0.3

Ant exclusion was relatively effective, we only collected a total of 49 ants in ALL and ANT understory treatments (which excluded ants) and 3 ants in the canopy. In contrast, 140 and 100 ants were found in VER and CN2 understory treatments respectively, accounting for approximately 7% of all collected arthropods, while only 4 ants were recorded in VER and CN2 in total in the canopy (Table S3.1).

In both the canopy and understory, only VER and ALL exclusions led to a significant increase in arthropod density (Figure 2a). Arthropod density increased by 82 % in VER and 53 % in ALL compared to the controls (z = -5.086, P < 0.001; z = 3.631, P = 0.001, respectively) (Table S3.2) in both the canopy and understory. The effect of ANT exclusion did not differ significantly from the control in both the canopy and the understory (Table S3.2 and Table S2.11).

Among the control treatment individuals, herbivory damage was significantly higher in the understory than in the canopy (W = 1290370, P < 0.001) with a 60 % increase in herbivory in the understory (Table 1).

In both the canopy and understory, only VER and ALL exclusions led to a significant increase in herbivory damage. In the canopy, herbivory increased by 42 % in VER and 36 % in ALL (Table S3.2) compared to the controls (z = -5.386, P < 0.001; z = 4.726, P < 0.001, respectively) (Figure 2b). In the understory, herbivory increased by 42 % and 35 % (Table S3.2) in comparison to the controls (P < 0.001) (Figure 2b). The effect of ANT exclusion did not differ significantly from the controls in both the canopy and understory (Table S3.2).

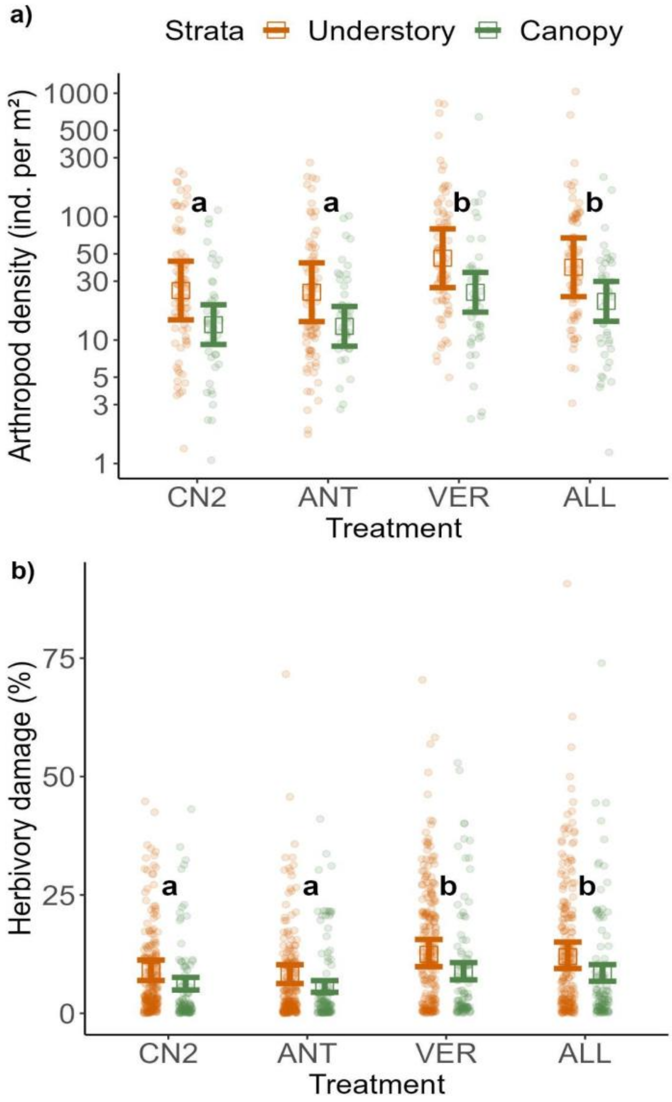

Figure 2: Total densities of all arthropods per square metre of foliage (a) and herbivory damage (%) (b) on surveyed saplings and branches of the CUVA (Canopy and Understory Vertebrate and Ant exclosure) experiment. Each individual data point represents (a) the density of arthropods or (b) the percentage of herbivory damage on either a canopy branch (green) or sapling individual in the understory (orange). The y-axis of (a) is on a log scale. Square and whiskers mark estimated marginal means and standard errors of the most parsimonious model.

Significant pairwise comparisons between predictors were tested by Tukey post hoc tests and are indicated with letters (note that the results are the same for canopy and understory). CN2 = control treatment, ANT = ant exclosure, VER = vertebrate exclosure, ALL = all predator exclosure.

Arthropod density and herbivory damage after the UBB experiment

In total, we collected 2,544 arthropods from 240 saplings across 8 plant species at the end of the UBB experiments (i.e., two years combined). The exclusion of birds led to a significant increase in mean arthropod density by 89 % in comparison to the control trees ($z = 3.789$, $P < 0.001$). Similarly, in the absence of bats, arthropod density increased significantly by 63 % in comparison to the control saplings ($z = 2.876$, $P = 0.012$) (Figure 3a).

However, only the exclusion of birds led to significantly increased mean herbivory damage ($z = 2.827$, $P = 0.013$) by 28% in comparison to the controls (Figure 3b). The effect of bat exclusion was detectable (+ 22% in comparison to the control) but non-significant ($z = 2.221$, $P = 0.067$).

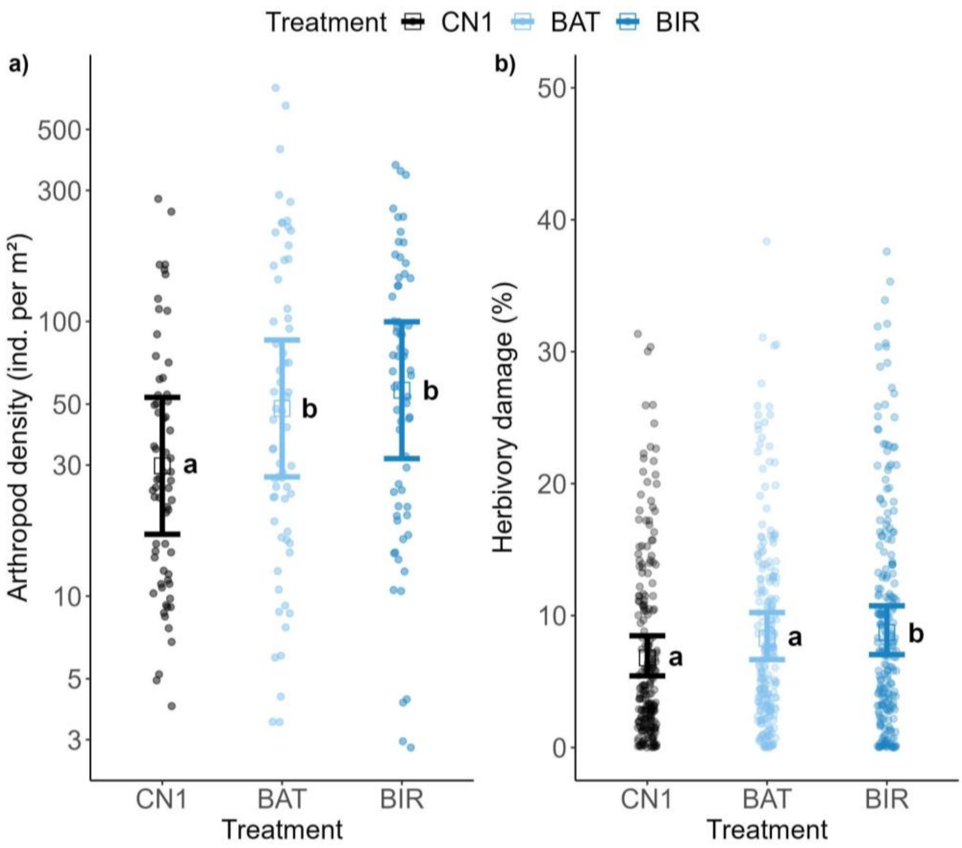

Figure 3: Effects of the exclusion of birds and bats on the total densities of all arthropods per square metre of foliage (a) and on the herbivory damage of individual saplings (b) of the UBB (Understory Bird and Bat exclusion) experiment. Individual data point represents a density of arthropods (a) or herbivory damage (b) on an individual sapling. The y-axis of (a) is on a log scale. Square and whiskers mark estimated marginal means and standard errors of the most parsimonious model. Significant pairwise comparisons between predictors were tested by Tuckey post hoc tests and are indicated with letters. Note that four extreme values of herbivory have been removed from the BIR raw data for visualisation purposes (b). CN1 = control treatment, BAT = bat exclosure, BIR = bird exclosure.

Arthropod feeding guilds

During the CUVA experiment, sapsuckers were the most abundant feeding guild (5403 individuals), found on 48% of saplings and branches, followed by no relationship arthropods

(2231, present on 73%), predators (1865, present on 84%), and leaf chewers (1150, present on 58%). In the UBB experiment, predators (894, present on 89% of saplings) and sapsuckers (662, present on 68% of saplings) were dominant, followed by leaf chewers (526, present on 72%) and NR (462, present on 57%).

Across the CUVA experiment, only the sapsucker ($z = 3.531$, $P = 0.001$; $z = 4.547$, $P < 0.001$) and NR ($z = 2.529$, $P = 0.032$; $z = 2.575$, $P = 0.028$) arthropods exhibited significant increases in their densities, with increments of 297% and 161% after the exclusion of vertebrates (VER) and 504% and 166% after the exclusion of all predators (ALL), respectively (Figure 4a). Additionally, the exclusion of ants (ANT) resulted in a significant 64% reduction in the densities of predatory arthropods ($z = -2.442$, $P = 0.041$). None of the exclusions had a significant impact on chewer densities (Table S3.3). It is important to note that the strata did not exhibit significant interactions with the treatments for any of the arthropod densities (Table S2.2); therefore, they were not considered in these results.

At the end of the UBB experiment, the NR ($z = 2.17$, $P = 0.058$; $z = 2.94$, $P = 0.007$) significantly increased their densities after excluding bats and birds independently by 285 and 517 % respectively. In addition, the sapsucker arthropods significantly increased their densities by 741 % after the removal of birds ($z = 2.84$, $P = 0.009$). Neither the chewers nor the predatory arthropods significantly changed their densities after the exclusion of bats and birds (Figure 4b).

We did not find significant differences in the densities of total arthropods ($W = 1491$, $P = 0.545$) and predatory arthropods ($W = 1626$, $P = 0.887$) between controls (CN2) and frame-controls (FCN2) (Figure S3.2, S3.3, respectively).

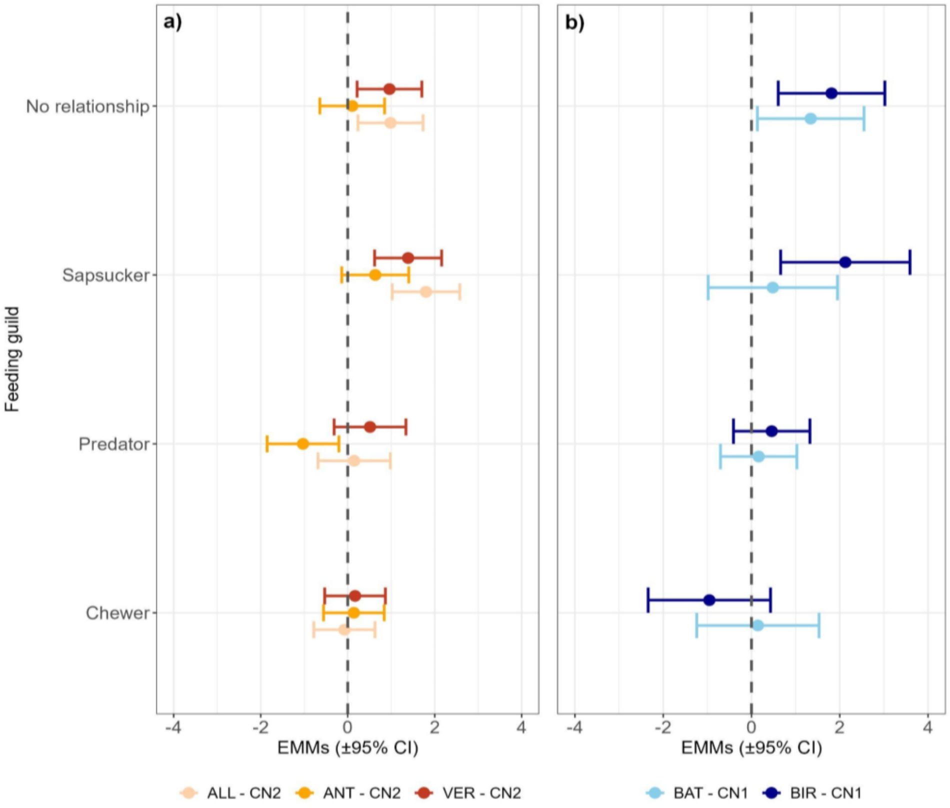

Figure 4: Caterpillar plot showing how the feeding guilds (predatory arthropods, chewing herbivores, sapsucking herbivores and NR) respond to (a) all (ALL, beige), ant (ANT, orange) and vertebrate (VER, red) exclusion treatments in the CUVA (Canopy and Understory Vertebrate and Ant exclosure) experiment using canopy and understory data combined and to (b) bat (BAT, light blue) and bird (BIR, dark blue) exclusion treatments in the UBB (Understory Bird and Bat exclusion) experiment (understory only). The X-axis shows the estimated marginal means (EMMs) of each treatment against the control (dashed line = no change from control) with a 95% confidence interval of the most parsimonious model including the variable treatment. When the confidence interval is strictly above or below the dashed line, the effect is significant. CN2 = control treatment for the CUVA experiment. CN1 = control treatment for the UBB experiment.

Vertebrate and arthropod predators

Overall, we identified a total of 22 insectivorous bird species comprising 1,167 bird calls using point counts and recordings (i.e., two methods combined), as well as 5 insectivorous bat species consisting of 79 bat passes from recordings and 7 ant species from 908 individuals caught on baits (Table S3.4). The surveys conducted across different strata revealed that insectivorous birds were 139 % more abundant in the canopy than in the understory whereas insectivorous bat activity and ant abundance were 238 and 1,264 % greater in the understory than in the canopy (Figure 5a). For insectivorous birds, species richness was similar within strata, while a greater number of ants and bats (i.e., 40 and 33 % more species, respectively) were found in the understory (Figure 5b). In addition, bird biomass was 90% greater in the canopy than in the understory, whereas bat biomass was 258% greater in the understory than in the canopy (Figure 5c).

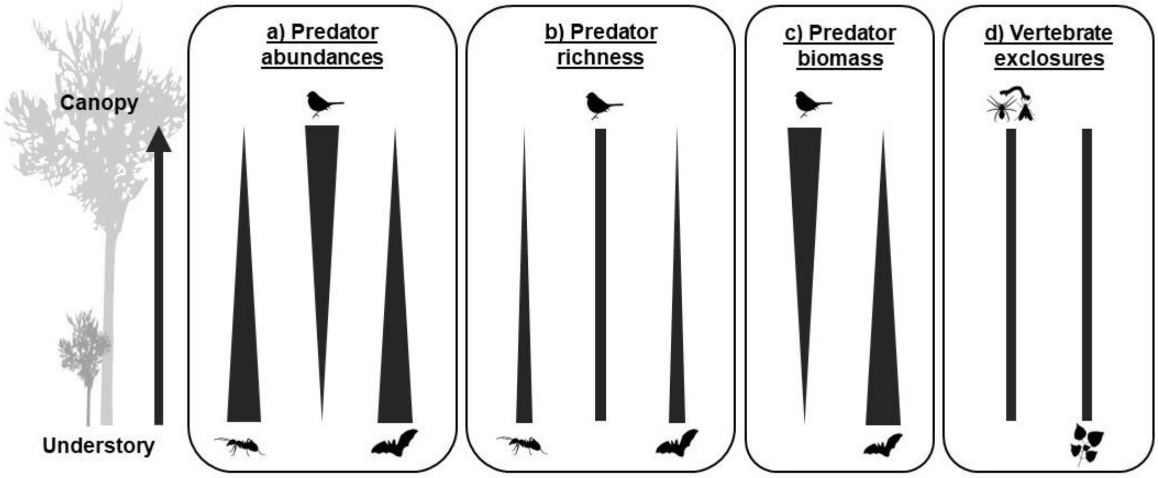

Figure 5: Simple comparisons between canopy and understory levels for (a) insectivorous predator abundances (ants, birds, bats) (b) richness (ants, birds, bats) (c) biomass (birds and bats) (d) CUVA (Canopy and Understory Vertebrate and Ant) exclosure experiment results (effect on arthropod densities and herbivory damage in VER). Note that the size of the arrow depends on the magnitude of the difference between the canopy and the understory.

Discussion

Vertebrate predators (i.e., birds and bats together), but not ants, played a crucial role in preventing arthropod outbreaks and indirectly protecting plants from herbivory damage. Our results reveal that their effect was similarly strong in both the forest canopy and understory. Specifically, the absence of vertebrates led to nearly double the density of arthropods, indirectly increasing the herbivory damage by almost half, regardless of the strata. Additionally, the individual effects of the bird, bat and ant exclusions demonstrated an antagonistic rather than an additive impact on arthropod density. Our study underscores the significance of vertebrate predator presence in maintaining the equilibrium of trophic cascades in both the canopy and understory of temperate ecosystems. These findings contribute to our understanding of the role of stratification in trophic cascades within temperate regions, an aspect that has been relatively unexplored in previous research (Aikens et al., 2013; Böhm et al., 2011).

The density of arthropods observed on control individuals revealed that there were globally more arthropod individuals per leaf area in the understory. This trend was particularly pronounced among predatory arthropods in contrast to chewers, aligning with the established notion that vertical stratification of herbivores in temperate forests is relatively weak (Basset, 2003). Higher abundances or densities of arthropods in the understory have been attributed to various factors, including the greater stability of the microclimate closer to the ground (Parker et al., 1995), dispersal limitation after emergence (Brown, 1997) and the distribution of quality food resources (Basset, 2003). In line with the trend in arthropod distribution, we observed a 60 % increase in herbivory damage on understory control saplings when compared to canopy control branches. Additionally, mean herbivory damage was approximately 8% in our study, which closely matches the findings from previous studies in temperate forests, which typically report herbivory damage levels around 5-10% (Gossner et al., 2014; Reynolds & Crossley, 1997; Wang et al., 2016).

In contrast to our first hypothesis **[H1]**, which postulated that predators would have a strong and additive effect on arthropod communities, our results indicate that vertebrate predators (VER) and ants (ANT) exhibit antagonistic effects when compared to the combination of vertebrate predators with ants (ALL). Similarly, bats (BAT) and birds (BIR) show antagonistic effects when compared to vertebrate predators (VER). This could imply that despite their differing activity periods, birds and bats may be partially competing for the same prey resources. Indeed, birds and bats both display a preference for large prey (Philpott et al., 2004; Sam et al., 2023; Sivault et al., 2023; Van Bael et al., 2003), potentially leading to a constraint in prey availability, thereby diminishing their collective effect. On the other hand, it is possible that the differing collection times of the two experiments (i.e., a one-month difference) might account for the observed pattern (Figure 6). We collected arthropods from the VER exclosures later in the season, which could lead to differences in prey availability and size.

Furthermore, during the UBB and CUVA experiments, BIR, BAT, VER, and ALL treatments significantly prevented arthropod outbreaks in both the canopy and understory, whereas the ANT treatment did not. These results contrast with previous studies in temperate forests where ants were shown to reduce the abundance of nearby insects (Gras et al., 2016; Sanders & van Veen, 2011). Looking at the ant species found during our surveys (Table S3.4), all of them are generalists, suggesting that ants were not a particularly important mesopredator in our system. In fact, their mutualism with sap-sucking insects may have been more relevant than their potential role as mesopredators in our study (Offenberg, 2001). Furthermore, the relative abundance of ants (ca. 7% of all arthropods) can make them important prey items for vertebrates.

Both the results of the UBB and CUVA experiments also showed that the removal of vertebrates mainly affected the densities of NR arthropods and sapsuckers, but not chewers and mesopredators (Figure 6). Indeed, in treatments where birds were absent (VER, ALL, and BIR exclosures), we observed an increase in sapsucker densities but not in mesopredator densities, indicating that this is the result of direct consumption by birds. This was unexpected, as we did not anticipate birds to feed abundantly on sapsuckers. Their small size and sessility likely make them inconspicuous to vertebrate insectivores. Although, this observation is consistent with recent findings in tropical areas (Ferreira et al., 2023; Ocampo-Ariza et al., 2023). The lack of effects on chewers appears to be related to the difference in time frame between the two experiments. Due to the necessary duration constraints of the CUVA experiment required for the effective accumulation of predator and herbivore effects, the arthropod collection occurred after the peak of caterpillar abundances observed previously in similar Japanese forests (Murakami, 2002; Sayama et al., 2012; Verboven et al., 2001). Therefore, we did not collect many chewers at the end of the CUVA and UBB experiments, diminishing the overall effects of treatments on chewers.

In contrast, ant exclusion led to a significant reduction in mesopredator densities. This could be because ants were classified as mesopredators in our study, and their removal may impact the overall mesopredator pattern. Additionally, ants can serve as an important food source for other predatory arthropods through myrmecophagy, such as spiders (Aranea), bugs (Heteroptera; Brandt & Mahsberg, 2002), net-winged insects (Neuroptera), or flies (Diptera; Aceves-Aparicio et al., 2022; Wilson, 2000).

Our results were also inconsistent with **[H2]**, vertebrate predators did significantly contribute to the reduction of herbivory damage, but the effect of ants was not detectable in the CUVA experiment (Figure 6). The 42 % increase in herbivory in the vertebrate exclosures, compared to the controls, was comparable to the change in herbivory damage found after vertebrate predator exclusion in a German canopy (ca. 23 to 44%; Böhm et al., 2011), but greater than in other temperate canopies (ca. 0-15 %; Barber & Marquis, 2009; Beilke &

O'Keefe, 2023; Lichtenberg & Lichtenberg, 2002) and understories (ca. 0-18%; Barber & Marquis, 2009; Dekeukeleire et al., 2019; Maguire et al., 2015). The UBB experiment also revealed that bird exclosures alone led to an indirect increase in herbivory damage, whereas bat exclosures had a detectable but non-significant impact on herbivory. Nevertheless, the effects of birds and bats on herbivory seemed to be additive. It is possible that the effect on herbivory damage was more detectable than changes in arthropod densities, as herbivory accumulated throughout the experiments, whereas arthropod collection was confined to a specific day.

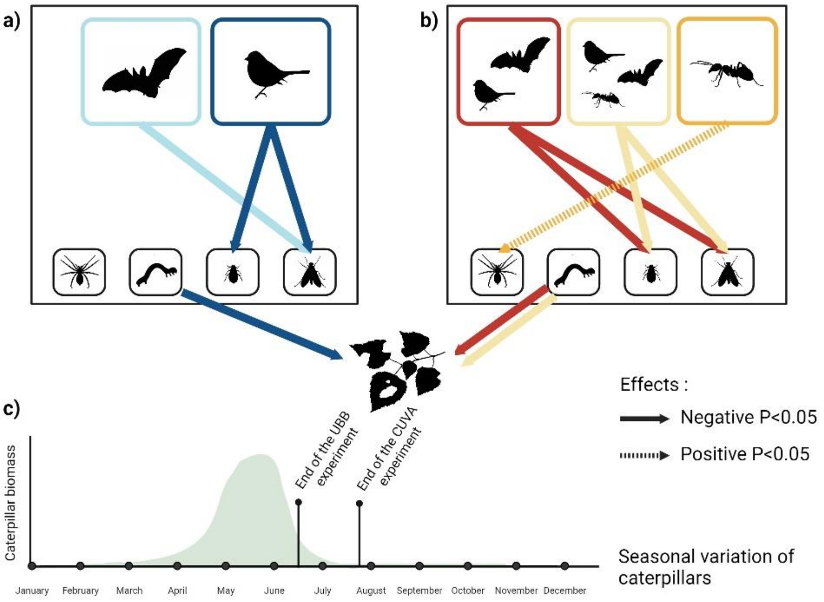

Figure 6: Distinct effects of bats and birds (UBB experiment - Understory Bird and Bat exclosure) (a), combined (VER), combined with ants (ALL) or predatory ants alone (ANT) (CUVA experiment - Canopy and Understory Vertebrate and Ant exclosure) (b) on mesopredators (spider), chewers (caterpillar), sapsuckers (aphid), NR (fly) densities and herbivory damage (leaf) (canopy and understory combined). Effects were assessed through generalised linear mixed models (GLMMs) (Table S2.2 and Table S2.9). The generic seasonal variation of caterpillar biomass in Japan, accompanied by the time frame of our experiments, is

depicted at the bottom of the plot, following the results of Verboven et al. (2001), Murakami (2002), and Sayama et al. (2012) (c).

Finally, in contrast to the third hypothesis **[H3]**, which posits that the effect of ants will be more pronounced in the understory and the effects of vertebrate predators in the strata with higher arthropod densities, our observations revealed that ants had no effects on arthropods or herbivory in both strata while vertebrate predators had similar impacts in the forest canopy and understory. This result aligns with other studies from temperate forests where vertebrate predation pressure on arthropods did not differ between vertical strata (Aikens et al., 2013; Boege & Marquis, 2006). Yet, it contradicted the optimal foraging theory, as we observed lower arthropod densities in the canopy than in the understory. Our predator surveys revealed that the abundance of insectivorous birds was 140% higher in the canopy than in the understory. In contrast, bats and ants were found to be the most abundant and rich in the understory. Therefore, the similar impacts on arthropods observed across strata may be attributed to the balanced predation pressure, with an increased presence of birds in the canopy and greater abundances of bats in the understory. Nevertheless, it is important to note that the bat sampling effort is much lower than that for birds in this study, as such, these results warrant a nuanced interpretation. Unfortunately, due to logistical challenges in conducting the study in the canopy, we could not differentiate between bird and bat predation in that area. It was impossible to remove and re-install the nets on a daily basis using the canopy crane. Future studies should explore ways to overcome this issue.

We recognize several methodological limitations in our study. Specifically, the individual trees selected may not adequately represent the entire tree communities in the forest and should be regarded only as a proxy. Our comparisons were constrained to young saplings and branches of mature trees, which are two models with markedly different characteristics. Mäntylä et al. (2011) observed no distinctions in the strength of top-down control on resulting herbivory between adult trees and saplings. Nonetheless, there are studies suggesting, for instance, that saplings may host more herbivores than mature trees (Böhm et al., 2011) due to lower concentrations of secondary metabolites (e.g., tannins). On the other hand, mature trees can be more conspicuous for both herbivores and insect predators than smaller saplings in the forest understory (Zverev et al., 2017). Overall, limited research exists on herbivory levels in the understory and canopy of temperate forests (but see Gossner et al., 2014; Reynolds & Crossley, 1997; Wang et al., 2016 for herbivory levels in temperate understories). Therefore, further research is necessary to determine if this observed pattern is consistent across other temperate forests.

Conclusion

Our study demonstrates that birds and bats, but not ants, play a crucial role in reducing arthropods in both the temperate forest canopy and understory, leading to a significant decrease in plant damage. Given that insectivorous bats and birds are present in numerous terrestrial ecosystems (Kunz et al., 2011; Whelan et al., 2008), the importance of their predation likely extends to many other areas. In addition, being threatened by various factors worldwide such as habitat loss, hunting, and the impacts of climate change (Benitez-Lopez et al., 2017; Donald et al., 2001; Stephens et al., 2016), it is imperative that we prioritise the conservation of these essential predators. This work also prompted several exciting follow-up considerations that could deepen our understanding of the intricate relationships between bats, birds, insects, and plant communities. For instance, exploring how these effects change in tropical forests, and understanding the impact of bottom-up control on the patterns found here. It was shown that the predation rate by ants strongly changes with increasing latitude, suggesting a potentially more pronounced impact in tropical regions (Zverava et al, 2020), than what we have observed in this temperate study. Additionally, the effects of top-down and bottom-up forces on generalist and specialist herbivores differ, with bottom-up forces exerting stronger effects on specialists (Vidal & Murphy, 2017). Hence, future studies must consider the role of bottom-up forces to encompass a critical aspect of most ecological interactions.

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Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

Elise Sivault, Jan Kollross, Sam Finnie, Sara Fernandez Garzon, Jan Lenc, Martin Libra, Masashi Murakami, Tatsuro Nakaji, Masahiro Nakamura, Rachakonda Sreekar, Legi Sam, Tomokazu Abe and Katerina Sam conducted the fieldwork and collected the data; Matthias Weiss and Jan Kollross led the arthropod sorting and identification; Katerina Sam and Heveakore Maraia led the leaf herbivory analysis with the support of several undergraduate students; Elise Sivault, Sara Fernandez Garzon and Rachakonda Sreekar led the bat, ant and bird surveys, respectively; Elise Sivault and Leonardo Re Jorge performed the data analyses; Katerina Sam designed and funded the study and helped with the analyses; Elise Sivault and Jan Kollross wrote the first draft of the manuscript. All authors contributed significantly to revisions and gave final approval for publication.

Statement on inclusion

Our study brings together authors from a number of different countries (including developing countries), including scientists based in the country where the study was carried out. All authors were engaged early on with the research and study design to ensure that the diverse sets of perspectives they represent was considered from the onset. The study involved six Ph.D. students, four postdoctoral researchers, and three female researchers. Whenever relevant, literature published by scientists from the region was cited.

Data availability statement

The data supporting the results will be archived in the public repository Dryad if the paper is accepted for publication and the data DOI will be included at the end of the article.

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Supporting information

Appendix S1

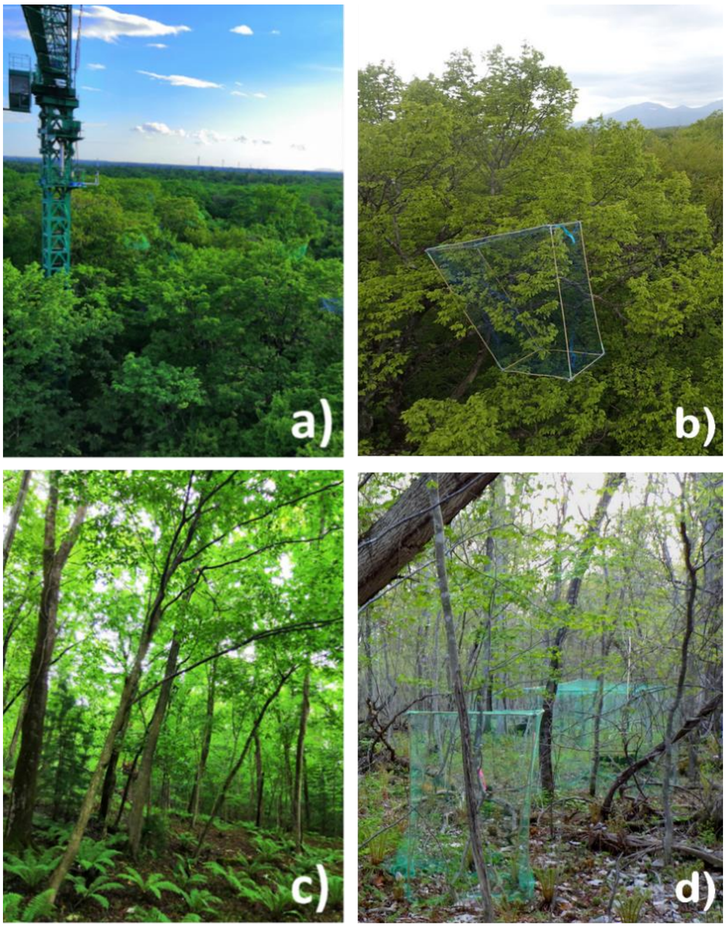

Figure S1.1: Photos depicting (a) the characteristic forest canopy (with several detectable vertebrate exclosures) (c) the understory in the study area (b) the vertebrate exclosure treatment attached within the canopy and (d) the vertebrate exclosure treatments situated in the understory. Photographed by Jan Kollross.

Table S1.1: Plant species used in the UBB (understory species) and the CUVA experiments (both understory and canopy species).

Family	Plant species	Understory	Canopy
Magnoliaceae	*Magnolia kobus*	X	X
Oleaceae*	*Syringa reticulata*	X	
Betulaceae	*Carpinus cordata*	X	X
Sapindaceae	*Acer mono*	X	X
Rosaceae	*Prunus ssiori*	X	X
Sapindaceae	*Acer palmatum*	X	X
Oleaceae	*Fraxinus lanuginosa*	X	X
Betulaceae**	*Betula maximowicziana*	X	
Betulaceae**	*Ostrya japonica*		X

*Note that *Syringa reticulata* was absent from the canopy, resulting in a difference in the number of tree species between the canopy and understory in the CUVA experiment. **Note that *Betula maximowicziana* never grew taller than 3 m in the experimental forest, and *Ostrya japonica* rarely occurred as reachable saplings. Therefore, these two species were paired for the purpose of the CUVA experiment.

Table S1.2: Study design in CUVA experiment. Overview of the treatments within the experiment, their location, number of species and individuals used in each of them and experiment duration.

Strata	Treatment	Species	Individuals per species and treatment	Duration (days)
Understory	VER–exclusion of vertebrates	8	5	65 ± 4
Understory	ALL- exclusion of ants and vertebrates	8	5	65 ± 4
Understory	ANT- exclusion of ants	8	5	65 ± 4
Understory	CN2- control	8	5	65 ± 4
Understory	FNC2 - frame-control	8	5	65 ± 4
Canopy	VER– exclusion of vertebrates	7	3	65 ± 4
Canopy	ALL- exclusion of ants and vertebrates	7	3	65 ± 4
Canopy	ANT- exclusion of ants	7	3	65 ± 4
Canopy	CN2-control	7	3	65 ± 4

Table S1.3: Study design in UBB experiment. Overview of the treatments within the experiment, their location, exclosure manipulation, number of species and individuals used in each of them and experiment duration.

Strata	Treatment	Exclosure closed	Species	Individuals per species and treatment	Duration (days)
Understory	BIR – exclusion of birds	Night	8	5	30 ± 2
Understory	BAT- exclusion of bats	Day	8	5	30 ± 2
Understory	CN1- control	-	8	5	30 ± 2

Table S1.4: Starting and ending dates of both experiments (CUVA and UBB experiments) in the years 2018 and 2019.

Experiment	Year	Start	End
UBB	2018	20-23.5.	19-22.6.
	2019	12-15.5.	11-14.6.
CUVA	2018	12-22.5.	22-31.7.
	2019	17.5.-8.6.	20-29.7.

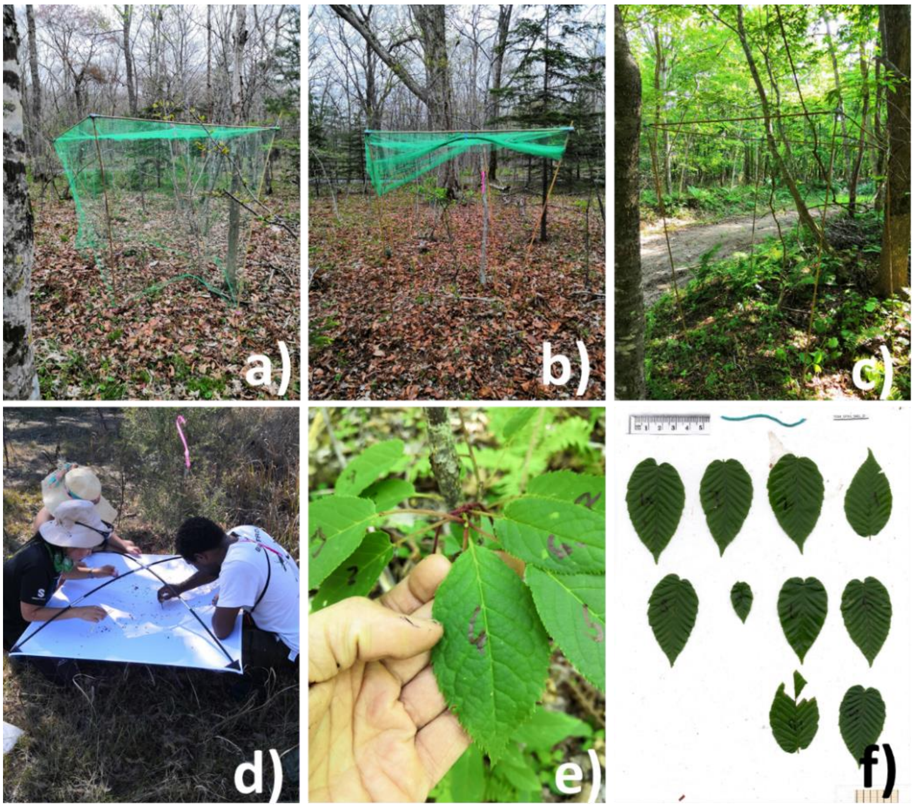

Figure S1.2: Photos depicting (a) the vertebrate exclosure treatment in the forest understory, (b) the bird and bat exclosure treatment, with the mesh pulled up allowing the entrance of birds during the day (or bats during the night), (c) the FCN2 construction treatment, (d) the collection of the arthropods from the beating sheet at the end of the experiment, (e) the red string marked twig with numbered leaves ready for the collection at the end of the experiment and (f) the scanning of the leaves at the end of the experiment. Photographed by Jan Kollross and Elise Sivault.

Appendix S2

Table S2.1: Comparisons of multi-predictor models analysing factors (i.e., treatment and strata) affecting the density of all arthropods and herbivory damage, in the CUVA experiment. Results of the analysis of deviance based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in bold, and the selected models are indicated in grey. Note that the second-best model has been selected for arthropod densities due to multicollinearity issues.

	Arthropod densities		Herbivory damage	
	dAICc	df	dAICc	df
Null	90.3	5	91.2	6
Treatment	61.5	8	37.8	9
Strata	68.9	6	61.6	7
Strata + Plant species:Strata	35.4	8	60.6	9
Treatment + Strata	38.1	9	3.1	10
Treatment + Strata + Plant species:Strata	0.5	11	**0.0**	**12**
Treatment * Strata	37.6	12	6.1	13
Treatment * Strata + Plant species:Strata	**0.0**	**14**	3.1	15

Table S2.2: Comparisons of multi-predictor models analysing factors (i.e, treatment and strata) affecting the density of leaf chewers, predators, sapsuckers and NR (i.e., arthropod with no consumptive effect on other arthropods or plants) in the CUVA experiment, based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in bold and the selected models to plot the graphics are indicated in grey. Note that the selected model for chewer density had to contain the variable treatment for visualisation purposes (Figure 4).

	Chewer densities		Predator densities		Sapsucker densities		NR densities	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Null	**0.0**	**5**	21.5	5	23.6	5	5.7	5
Treatment	5.5	8	13.2	8	7.2	8	0.1	8
Strata	1..9	6	8.5	6	18.5	6	5.7	6
Strata + Plant species: Strata	4.0	8	9.5	8	17.9	8	8.4	8
Treatment + Strata	7.4	9	**0.0**	**9**	1.3	9	**0.0**	**9**
Treatment + Strata + Plant species: Strata	9.6	11	0.9	11	**0.0**	**11**	2.6	11
Treatment* Strata	9.2	12	5.8	12	1.3	12	4.2	12
Treatment * Strata + Plant species: Strata	11.5	14	6.7	14	0.1	14	6.8	14

Table S2.3: Estimated marginal means (=emmeans) of the CUVA experiment models including arthropod density and herbivory damage as response variables. Note that the arthropod density data were log-transformed prior to the analyses.

Arthropod density			
Treatment-Strata	emmean	SE	df
ALL-Canopy	-6.19	0.173	13.4
ANT-Canopy	-6.65	0.172	13.1
CN2-Canopy	-6.62	0.172	13.1
VER-Canopy	-6.02	0.172	13.1
ALL-Understory	-5.55	0.249	11.2
ANT-Understory	-6.02	0.249	11.2
CN2-Understory	-5.98	0.249	11.2
VER-Understory	-5.38	0.249	11.2
Herbivory			
ALL-Canopy	0.08	0.008	1327
ANT-Canopy	0.05	0.006	1327
CN2-Canopy	0.06	0.006	1327
VER-Canopy	0.08	0.009	1327
ALL-Understory	0.11	0.014	1327
ANT-Understory	0.08	0.010	1327
CN2-Understory	0.08	0.010	1327
VER-Understory	0.12	0.014	1327

Table S2.4: Estimated marginal means (=emmeans) of the CUVA and UBB experiment models including predator density as a response variable. Note that the data were log-transformed prior to the analyses.

Predator density			
Treatment	emmean	SE	df
ALL	-8.45	0.429	31.4
ANT	-9.63	0.426	30.4
VER	-8.09	0.426	30.4
CN2	-8.60	0.426	30.4
BIR	-6.95	0.405	28.2
BAT	-7.24	0.405	28.2
CN1	-7.41	0.405	28.2

Table S2.5: Estimated marginal means (=emmeans) of the CUVA and UBB experiment models including chewer density as a response variable. Note that the data were log-transformed prior to the analyses.

Chewer density			
Treatment	emmean	SE	df
ALL	-10.02	0.319	37.3
ANT	-9.80	0.316	36.0
VER	-9.77	0.316	36.0
CN2	-9.94	0.316	36.0
BIR	-9.84	0.672	25.6
BAT	-8.74	0.672	25.6
CN1	-8.89	0.672	25.6

Table S2.6: Estimated marginal means (=emmeans) of the CUVA and UBB experiment models including sapsucker density as a response variable. Note that the data were log-transformed prior to the analyses.

Sapsucker density			
Treatment	emmean	SE	df
ALL	-9.73	0.307	74.9
ANT	-10.90	0.303	71.5
VER	-10.15	0.303	71.5
CN2	-11.53	0.303	71.5
BIR	-8.37	0.796	20.1
BAT	-10.02	0.796	20.1
CN1	-10.50	0.796	20.1

Table S2.7: Estimated marginal means (=emmeans) of the CUVA and UBB experiment models including NR density (i.e., arthropod with no consumptive effect on other arthropods or plants) as a response variable. Note that the data were log-transformed prior to the analyses.

NR density			
Treatment	emmean	SE	df
ALL	-8.42	0.311	58.1
ANT	-9.30	0.308	55.9
VER	-8.44	0.308	55.9
CN2	-9.40	0.308	55.9
BIR	-9.11	0.519	36.9
BAT	-9.58	0.519	36.9
CN1	-10.93	0.519	36.9

Table S2.8: Results of the analysis of deviance examining the effect of the explanatory variable treatment on densities of all arthropods and herbivory damage, in the UBB experiment, based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in bold and the selected models to plot the graphics are indicated in grey.

	Arthropod densities		Herbivory damage	
	dAICc	df	dAICc	df
Null	11	4	4.9	5
Treatment	**0**	**6**	**0.0**	**7**

Table S2.9: Results of the analysis of deviance examining the effect of the explanatory variable treatment on densities of chewers, predators, sapsuckers and NR (i.e., arthropod with no consumptive effect on other arthropods or plants), in the UBB experiment, based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in bold and the selected models to plot the graphics are indicated in grey. Note that the selected model for chewer and predator densities had to contain the variable treatment for visualisation purposes (Figure 4).

	Chewer densities		Predator densities		Sapsucker densities		NR densities	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Null	**0.0**	**4**	**0.0**	**4**	4.6	4	5	4
Treatment	1.4	6	3.1	6	**0.0**	**6**	**0.0**	**6**

Table S2.10: Estimated marginal means (=emmeans) of the UBB experiment models including arthropod density and herbivory damage as response variables. Note that the arthropod density data were log-transformed prior to the analyses.

Arthropod density			
Treatment	emmean	SE	df
BAT	-5.33	0.265	12.7
BIR	-5.18	0.265	12.7
CN1	-5.82	0.265	12.7
Herbivory			
BAT	0.08276	0.009058	683
BIR	0.087143	0.009375	683
CN1	0.067925	0.007715	683

Appendix S3

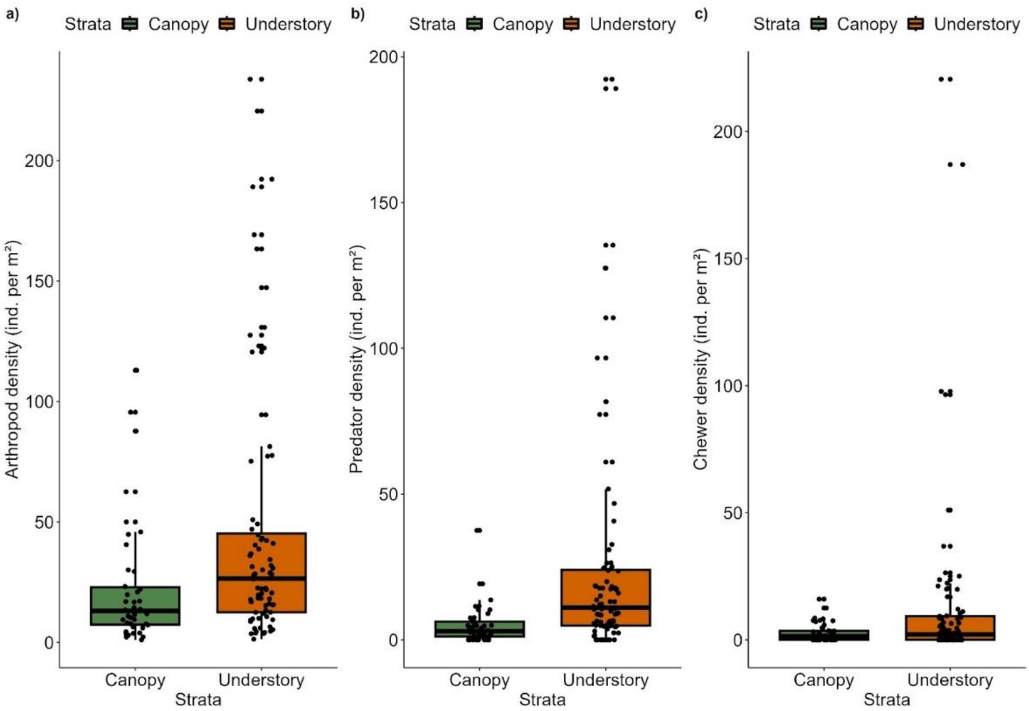

Figure S3.1: Total arthropod densities (individuals per square meter of foliage) (a), predator (b) and chewer (c) densities between canopy and understory on control treatments (CN2) in the CUVA experiment. The differences between the two strata are significant for the total arthropod and predator densities only (W=2245, P=0.002 and W=2539, P<0.001 respectively).

Table S3.1: Number of ants collected at the end of the CUVA experiment in each treatment (ANT, ALL, VER, and CON) at the canopy and understory levels. Note that zero ants were expected for ANT and ALL treatments if the removal of ants was 100% successful.

Treatment	Canopy	Understory
ANT	1	13
ALL	2	36
VER	2	140
CON	2	100

Table S3.2: The percentage increase or decrease of arthropod density and herbivory damage between VER, ALL, and ANT treatments compared to CN2 (controls). The significance is marked as follows: * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

	Arthropod density		Herbivory damage	
	Canopy	Understory	Canopy	Understory
VER-CN2	82 %***	82 %***	42 %***	42 %***
ALL-CN2	53 %***	53 % ***	36 %***	35 %***
ANT-CN2	-2 %	-3 %	-9 %	-9 %

Table S3.3: Percentages of increases or decreases of arthropod density partitioned into feeding guilds (NR: arthropod with no consumptive effect on other arthropods or plants) between treatments and experiments (canopy and understory combined). The significance is marked as follows: * P ≤ 0.05, ** P ≤ 0.01, *** P ≤ 0.001.

	Chewers		Predators		Sapsuckers		NR	
	UBB	CUVA	UBB	CUVA	UBB	CUVA	UBB	CUVA
VER		18 %		66 %		297 % ***		161 %*
ALL		-7.6 %		16 %		504 % ***		166 %*
ANT		15 %		-64 %*		87 %		10 %
BIR	-61 %		58 %		741 %**		517 %**	
BAT	16 %		18 %		61 %		285 %*	

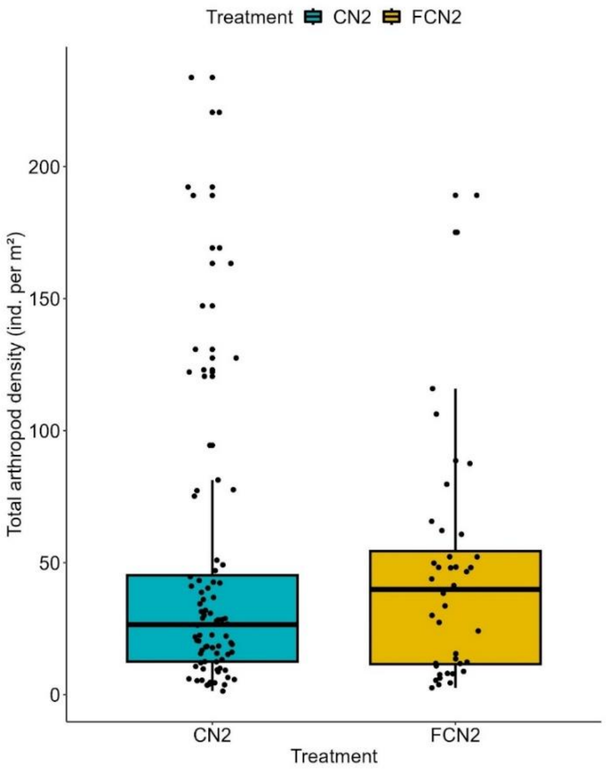

Figure S3.2: Total arthropod densities (individuals per square meter of foliage) between control (CN2) and frame-control (FCN2) in the understory (CUVA experiment). The difference in densities between the two controls is not significant ($P>0.05$).

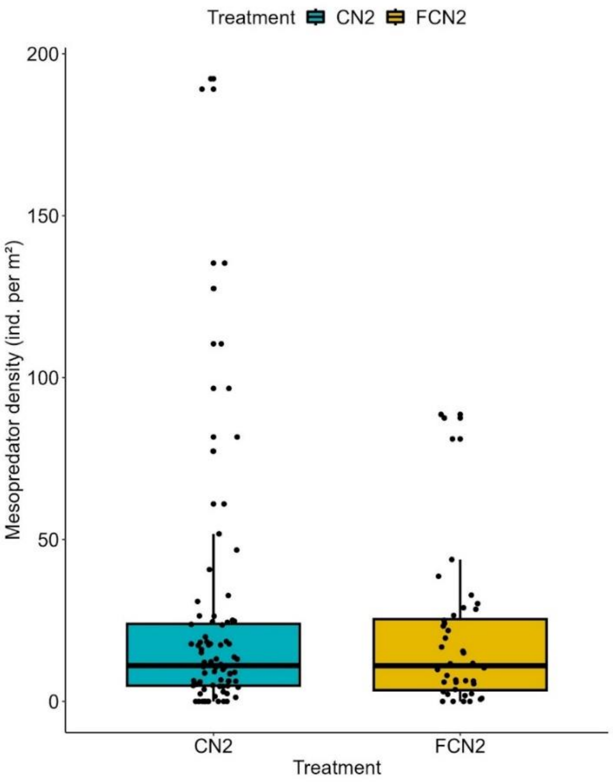

Figure S3.3: Mesopredator densities (individuals per square meter of foliage) between control (CN2) and frame-control (FCN2) in the understory (CUVA experiment). The difference in densities between the two controls is not significant ($P>0.05$).

Table S3.4: Results of the bird, bat, and ant surveys. For each species identified, abundance (ab.) or activity was estimated at each stratum. The body mass of the vertebrates (average or range) was found in the literature and used to calculate the biomass.

BIRDS			
Species	Canopy ab.	Understory ab.	Weight (avg.) (g)
Aegithalos caudatus	30	0	8.3
Anthus hodgsoni	8	1	21.6
Certhia familiaris	8	9	8.9
Cuculus optatus	22	6	106
Cyanoptila cyanomelana	0	9	25
Ficedula narcissina	89	63	11.5
Hierococcyx hyperythrus	2	0	120.1
Muscicapa dauurica	2	0	11.9
Paridae spp.	0	21	14.6
Parus minor	96	55	17
Periparus ater	93	20	9.6
Phylloscopus borealoides	17	0	10.7
Phylloscopus coronatus	203	24	9.2
Poecile palustris	54	10	11.9
Sitta europaea	25	3	22.5
Sittiparus varius	39	1	16.5
Turdidae sp.	0	1	70
Turdus cardis	5	22	65
Turdus chrysolaus	7	18	77
Urosphena squameiceps	0	63	9
Yungipicus kizuki	63	16	22
Zosterops japonicus	60	2	10.7
BATS			
Species	Canopy ab.	Understory ab.	Weight (range) (g)
Murina spp.	3	5	9-10.0

Myotis ikonnikovi	1	0	10
Myotis macrodactylus	0	6	6.0-8.0
Plecotus sacrimontis	1	0	7.4-9.2
Vespertilio sinensis	13	50	14-30
ANTS			
Species	Canopy ab.	Understory ab.	
Aphaenogaster japonica	0	2	
Camponotus obscuripes	0	9	
Lasius hayashi	31	102	
Lasius spathepus	24	48	
Myrmica ruginodis	4	357	
Nylanderia flavipes	2	281	
Pheidole fervida	1	47	

Chapter 5

Top-down control of herbivory intensifies towards the most bird and bat species-rich forests

Elise Sivault, Sara Fernández Garzon, Sam Finnie, Marketa Houska Tahadlova, Jitka Jančúchová Lásková, Leonardo Re Jorge, Jan Kollross, Jan Lenc, Martin Libra, Heveakore Maraia, Amelia Joyce Philip, Tereza Vlasatá, Matthias Weiss, Xue Xiao and Katerina Sam

Top-down control of herbivory intensifies towards the most bird and bat species-rich forests

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Abstract

Traditional ecological theories assume that the top-down forces acting on herbivores increase towards the equator, where predator populations are dense and diverse. However, it is likely that these forces vary on a site-specific basis due to local conditions. Our study is the first to compare multiple sites across latitudes using diurnal and nocturnal predator exclusion experiments. We set up predator exclosures in six temperate and tropical forests (Germany, Japan, China, Papua New Guinea, and Australia), each of them lasting one month. Arthropods were collected and herbivory damage was analysed. Results showed that both bats and birds reduced arthropod densities by ~70% to the same extent in all forests. Birds and bats also mitigated herbivory damage, particularly in warm temperate and tropical forests where protected saplings showed up to 500% less damage. Contrary to the effects of exclusion on arthropods, our findings on herbivory damage align with our expectations, showing an intensified top-down control of herbivory towards most bird and bat species-rich forests. This discrepancy highlights the need for further research into the intricate interplay between top-down and bottom-up influences. Yet, obtaining such strong effects only over one-month-long experiments is promising and provides baseline data for future research exploring broad-scale variations in trophic cascades.

Introduction

The idea that herbivore populations can be constrained not only by resource availability but also by interactions with higher trophic levels was introduced in the 1960s as the 'world is green hypothesis' (Hairston et al., 1960). Since then, natural enemies acting as top-down forces have gained widespread recognition as significant selective pressure on primary consumers, particularly herbivorous insects (Bernays & Graham, 1988; Mooney et al., 2012; Vidal & Murphy, 2018). However, despite this recognition, studies often overlook spatial variation, including local and landscape effects (Halaj & Wise, 2001; Mooney et al., 2010; but Sam et al., 2024). Consequently, numerous knowledge gaps remain regarding the relative importance of top-down forces in different habitats or climatic regions.

A commonly used approach to measure the effects of top-down forces across habitats is through predator exclusion experiments (Maas et al., 2019). Predator exclosures, in the form of cages, effectively restrict the access of insectivorous predators, especially flying vertebrates such as birds and bats, to plants. In most cases, these exclusion experiments have proven to be very effective as they exclude both birds and bats together (Böhm et al., 2011; Johnson et al., 2010; Karp & Daily, 2014; Maas et al., 2013; Nyffeler et al., 2018; Sam et al., 2022). Nevertheless, there has been an increasing trend in employing diurnal and nocturnal exclusions to differentiate the specific impacts of birds and bats (Bhalla et al., 2023; Bouarakia et al., 2023; Cassano et al., 2016; Gras et al., 2016; Kalka et al., 2008; Maas et al., 2013; Morrison & Lindell, 2012; Ocampo-Ariza et al., 2023; Williams-Guillén et al., 2008). These experiments have revealed negative effects of flying vertebrates on arthropod communities, attributed to bats alone (Cassano et al., 2016), birds alone (Gras et al., 2016), or both predators (Kalka et al., 2008; Maas et al., 2013; Morrison & Lindell, 2012; Ocampo-Ariza et al., 2023; Williams-Guillén et al., 2008).

In most of the predator exclusion studies, the change in arthropod density and communities due to the absence of predators has led to cascading effects on plants, resulting in foliar damage, fruit damage and yield reductions, either within diurnal exclusions only (Cassano et al., 2016; Gras et al., 2016) or in both types of exclusions (Bouarakia et al., 2023; Kalka et al., 2008; Morrison & Lindell, 2012; Ocampo-Ariza et al., 2023). However, in some cases, both bird and bat exclosures have been shown to release predatory arthropods (Cassano et al., 2016; Gras et al., 2016; Maas et al., 2013; Ocampo-Ariza et al., 2023). This mesopredator release (e.g., spiders, and ants) can mitigate the net effect of predator exclusions on plants, as demonstrated in Maas *et al.* (2013).

Previous studies have demonstrated that the effect of top-down forces on herbivores tends to increase towards the equator (Rodríguez-Castañeda, 2013; Roslin et al., 2017; Zvereva et al., 2020). This is consistent with the long-standing ecological concept that biotic interactions are generally more pronounced at low latitudes (MacArthur et al., 1972; Pennings & Silliman, 2005; Schemske et al., 2009). Highly productive ecosystems may have more resources available to support a greater number of predator species (Gillman et al., 2015), leading to potentially higher abundances of individuals within these species and, consequently, higher predation rates (Letourneau et al., 2009). For example, insectivorous bats and birds, like many other vertebrates, are expected to be more diverse in tropical forests than in temperate forests (Raz et al., 2023). In addition, greater diversity of predator species is also associated with increased functional diversity, raising the likelihood of highly efficient species being present (Duffy et al., 2007; Perfecto et al., 2004). For example, a foliage-gleaning species might be more effective in reducing herbivore communities (Kalka & Kalko, 2006). However, it is essential to note that this pattern is not universal, and there are exceptions influenced by factors such as limited resources, competition, and disturbances (e.g., Hendrickx et al., 2007; Wickramasinghe et al., 2004).

Indeed, the debate about the strength of top-down forces along the latitudinal gradient remains open. Borer *et al.* (2006) and Mooney *et al.* (2010) found that top-down forces do not vary with the productivity of the system (e.g., highest productivity in the tropics). Furthermore, with respect to the food web complexity, it is likely that top-down forces vary from site to site due to the landscape context (e.g., local biotic and abiotic conditions) (Gripenberg & Roslin, 2007). Despite these inconsistencies in the current data and knowledge gaps requiring attention, there are no comprehensive studies to date that have conducted extensive multi-site comparisons employing both diurnal and nocturnal exclosures, across different latitudes, within both tropical and temperate forests.

To address this gap, we conducted experiments to test the hypothesis that bats and birds play a role in trophic cascades within forest ecosystems by reducing arthropod density and thus indirectly decreasing forest defoliation caused by arthropods. We excluded birds and bats independently to investigate: (1) whether the absence of birds and bats leads to an increase in arthropod densities, (2) whether this increase leads to a change in herbivory damage, and (3) whether these effects correlate positively with the predator richness and abundance of the study site. We expected that saplings from which bats and birds were excluded would host a higher density of arthropods per leaf area and experience higher herbivory damage in comparison to the control saplings to which the predators had free access. Furthermore, we anticipated that these effects would be more pronounced at sites closer to the equator than at higher latitudes, where biotic interactions are stronger, and bird and bat populations are denser and more diverse.

Methods

Study sites

We conducted the experiments in six study sites (Figure 1) spanning from between 51° N and 33° S: a temperate floodplain forest in the Leipziger Auwaldkran (hereafter refer to as LAK, 2,500 hectares) in Leipzig, Germany (51°21'57.14" 12°18'34.05", 116m asl); a cool-temperate deciduous forest in the Tomakomai experimental forest (TOM, 2,720 hectares), the southern part of Hokkaido, Japan (42°40 '48.0" 141°35'24.0", 50m asl); a tropical seasonal rainforest in the Bubeng forest dynamic plot in the Xishuangbanna National Nature Reserve (BUB, 241,000 hectares), Yunnan Province, southwestern China (101°34′26.47″ 21°36′42.58″, 709-869m asl); a weakly seasonal lowland rainforest in the Kau Wildlife conservation area around Kakoba canopy crane (KAK, 300 hectares), Madang province, Papua New Guinea (-5° 8' 15.19" 145° 46' 30.28”, 100m asl); a lowland rainforest strongly seasonal in the Daintree Rainforest Observatory (DRO, 120,000 hectares), North Queensland, Australia (-16° 6' 20.15" 145° 26' 49.2", 40m asl) and an evergreen eucalyptus forest in the EucFACE facility of Western Sydney University (EUC, 35 hectares), New South Wales, Australia (-33° 36' 56.51" 150° 44' 25.33", 30m asl).

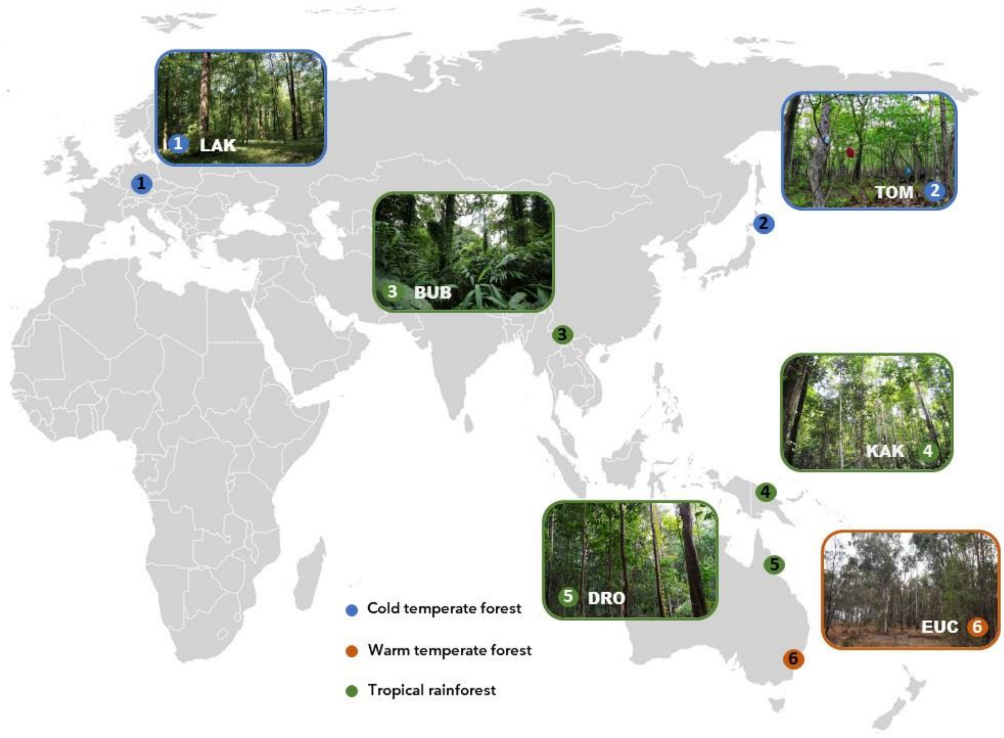

Figure 1: Map of the study sites classified per forest type (cold temperate, warm temperate or tropical). LAK: Leipziger Auwaldkran, Germany; TOM: Tomakomai experimental forest,

Japan; BUB: Bubeng forest dynamic plot, China; KAK: Kakoba canopy crane, Papua New Guinea; DRO: Daintree Rainforest Observatory, Australia; EUC: EucFACE facility, Australia. Photos of the forests taken by E. Sivault, J. Kollross, M. Houska Tahadlova.

Experimental set-up

The experimental design was derived from the “Understory Bird and Bat exclosure (UBB)” experiment described in Sivault *et al.* (2023) with a few modifications. In short, we preselected five, seven, or eight plant species per study site (Table S1.1 in Appendix S1) that were representative of the main lineages of trees present in each site. For each plant species, we identified suitable saplings (i.e., young trees, 1.5-2 m tall), and removed all arthropods from them, to reset the experiment to zero densities, ensuring similar starting conditions across all sites (i.e., we collected the arthropods in vials filled with ethanol, but did not use them in the analyses). We then randomly chose and marked three small twigs from each sapling. Each twig had at least ten leaves that we numbered. In all the study sites, we photographed the starting point of herbivory to later estimate only the herbivory that occurred during the experiment. In LAK and TOM, we initiated the experiment before the leaf flush, leading to initial herbivory levels close to zero. We assigned each sapling to one of three treatments: bird exclosure (BIR), bat exclosure (BAT), or control (CN1).

Exclosures were made of bamboo (in TOM) or PVC poles (in all other sites) (2 x 2 x 2.5m) covered by green netting with a mesh size of 3 x 3 cm which is similar to the mesh size of previous predator exclusion experiments (Greenberg et al., 2000; Houska Tahadlova et al., 2023; Sam et al., 2022; Van Bael et al., 2003). For BIR exclosures, the netting was pulled up at dusk to allow access to bats during the night and pulled down at sunrise to prevent access to birds during the day, and vice versa for BAT exclosures. Specifically, the nets were adjusted up or down during ±30 minutes around sunrise and ±30 minutes around sunset, aligning with the daily sunrise and sunset times at each study site. Our observations confirmed that the netting did not hinder the access of small insectivorous lizards and terrestrial mammals, although such occurrences were rarely observed. The controls (CN1) were saplings not enclosed by any constructions. Note that Sivault *et al.* (2023) demonstrated that the constructions alone do not attract significantly more arthropods than unenclosed controls (CN1).

To assure consistency in the experimental design, we applied each of the three treatments to 5 saplings per plant species, except in EUC, where we used twice as many saplings for *Acacia parramattensis* and *Eucalyptus tereticornis* due to the low number of plant species available in the forest (i.e., five species, Table S1.1). The experiment consistently lasted 30 ± 5 days at each site, during spring in temperate regions or at the onset of the wet season in tropical regions. The experiment was conducted twice: in 2018 and 2019 for TOM, DRO, and EUC, and in 2020 and 2021 for KAK, using a distinct set of saplings each year (Table S1.2). Due to the COVID-19 pandemic, our experiment was conducted only once in 2019 in BUB, as we were unable to return to China. To compensate for the disruption to the project timeline, we conducted the experiment in LAK in 2022 and doubled the number of saplings there.

Change in herbivory damage

To estimate only the herbivory that occurred during the experiment, we first measured the initial herbivory. Note that throughout the manuscript, herbivory is used as a proxy for chewing herbivory damage. At the beginning of the experiments, we photographed the numbered leaves of the selected twigs of each sapling. We then outlined any missing parts of leaves on the photographs in Photoshop® and calculated the remaining area (a) and the full expected area of each leaf (b), in cm² using ImageJ version 1.47 (National Institute of Health, USA) to calculate the total area eaten by herbivores (c), (c = b - a) per leaf. We then calculated the proportion of leaf area loss as c/b. The initial herbivory was identified as the mean proportion of leaf area loss per twig.

After completion of the experiments, to determine the final herbivory, we collected the twigs marked at the beginning of the experiments and scanned all the numbered leaves from it. We then repeated the same method used to measure the initial herbivory. In cases where a leaf was missing and clearly eaten (i.e., bits of the stalk or a tiny proportion of the leaf were found at the place where we would expect a numbered leaf), we filled in the dataset with the mean leaf size of the species and recorded 100% herbivory. The final herbivory was also identified as the mean proportion of leaf area loss per selected twig. To assess the changes in herbivory during the experiment only, we thus subtracted the initial herbivory from the final herbivory.

Arthropod collection

At the end of the experiment, we lowered the crown of each sapling above a beating sheet, shook the foliage and quickly captured all arthropods that had fallen on the sheet. We then inspected the leaves for any concealed arthropods and took notes on any arthropods that escaped during the beating process. We stored the arthropods in vials, which were later categorised into morpho-species, identified by their taxonomic order, and assigned to one of four feeding guilds: predator, leaf chewer, sapsucker, or no relationship (hereafter referred to as NR; arthropods with no consumptive effect on other arthropods or plants).

To calculate arthropod density, the number of arthropod individuals was determined per square metre of the total leaf area of the sapling. We estimated the total leaf area of each sapling based on the leaves collected for the herbivory assessment. We multiplied it by the total leaf count in each sapling using the mean value obtained from three independent estimations conducted by sampling technicians. Unfortunately, due to logistical issues, we were unable to collect arthropods in BUB; thus, this study site has been excluded from the analyses of arthropod densities.

Vertebrate predator data

To compare the study sites in terms of bird and bat richness and abundance, we estimated at each site, the bird richness and relative abundance from point counts, and the expected bird and bat richness using available online datasets. Shortly, point counts were carried out at 16 points regularly spaced along a 2,350-m transect at each study site; successive points were 150 ± 5 m apart to avoid overlap. All birds seen or heard within a fixed radius of 0–50 m were recorded (Sam et al. 2019), and the height of the individual above ground was noted. We started surveys 15 minutes before sunrise, and each count lasted 15 minutes so that all 16 points were surveyed before 11:00. All points were surveyed equally in 2019 (May 2019: TOM; August 2019: BUB; November 2019: DRO, EUC, KAK) and the survey was replicated nine-times (i.e., in 9 days). Unfortunately, we were not able to conduct point counts in LAK, thus, this study site has been removed from the analyses involving observed bird richness and relative abundance.

The list of expected bat and bird species was generated from the Map of Life public database (https://www.mol.org). We first delineated each study site area on the map, (i.e., forest area described earlier in the methods). Then, to determine the expected species richness at each site, we summed the species including occurrences within the area (i.e., occurrences are observations from public databases) and the species for which the area is part of their range (i.e., expert range maps). Given the limited information on the diet and foraging strategies of birds and bats in some of these areas, coupled with the potential influence of omnivorous and frugivorous birds and bats on herbivore behaviours (non-consumptive effects) or direct consumption (consumptive effects), we estimated the number of bird and bat species at each site, irrespective of their feeding guild and vertical stratification.

Statistical analysis

We first built linear mixed-effect models using the package "lme4" (Bates et al., 2015) to test the effect of treatment (factor of 3 levels: CN1, BAT, BIR), site (factor of 5 levels: LAK, TOM, KAK, DRO, EUC) and their interaction on log-transformed total arthropod densities (Table S1.3) (number of individuals per m² of foliage) and arthropod densities partitioned into four feeding guilds: leaf chewers, mesopredators, sapsuckers and no relationship (NR) (Table S1.4) and into six orders: Hemiptera, Hymenoptera, Coleoptera, Araneae, Orthoptera and Lepidoptera larvae (Table S1.5). All the models additionally contained the sampling year (factor of 2 levels) as a fixed effect and plant species (factor of 36 levels) as a random effect.

Then, we ran generalised linear mixed-effect models using the package 'glmmTMB' (Brooks et al., 2017) using a beta error distribution and the same predictors as above (except that site was a factor of 6 levels for this model) to model herbivory damage (mean final proportion - mean initial proportion of the leaf area lost for each twig) (Table S1.3). All the models contained the sampling year as a fixed effect and plant species (factor of 44 levels) and individual trees (factor of 1166 levels) as random effects.

Additionally, we aimed to investigate whether changes in arthropod density and herbivory damage between treatments correlate with predator richness and/or abundance at each study site. However, varying information was accessible for different sites. The observed bird richness and abundance data were not available for LAK, whereas the expected bird and bat richness was available for all the study sites. Consequently, we first built linear mixed-effect models to test the effect of treatment (factor of 3 levels), observed bird richness, observed bird abundance (both were estimated from point counts) and their interaction on log-transformed total arthropod densities (Table S1.6). All the models additionally contained the sampling year (factor of 2 levels) as a fixed effect and plant species (factor of 29 levels) and site (factor of 4 levels) as random effects. We, then, built generalised linear mixed-effect models using the same predictors to model herbivory damage. All the models contained the sampling year as a fixed effect and plant species (factor of 37 levels), site (factor of 5 levels) and individual trees as random effects.

We identified strong and positive correlations between the expected bird and bat richness across study sites (R = 0.84) (estimated from public databases) but also between the expected bird richness (R = 0.91) and bat richness (R = 0.98) with the observed bird richness (estimated from point-counts). Consequently, we ran the same models using the sum of expected bird richness and bat richness as a predictor (Table S1.7). In this model, data from all study sites were included.

To identify the best models, we generated all possible combinations of predictors. For the models including richness and abundance of predators, three-way interactions (richness:abundance:treatment) were excluded. All models, including the null model, incorporated random effects and sampling year as a fixed effect. We used the AICctab function from the 'bbmle' package (Bolker et al., 2017) to compute the corrected Akaike information criterion (AICc; Anderson & Burnham, 2002) for all models (refer to Table S1.3, S1.4, S1.5, S1.6, S1.7). For each best model, we obtained estimated marginal means (= emmeans) and comparisons among all variable levels, using the 'emmeans' package (Lenth & Lenth, 2018) and ran an analysis of variance. We controlled the model's quality and fit with the 'performance' package (Lüdecke et al., 2021).

Results

Total arthropod densities

In total, we collected 15,004 arthropods from 1,061 saplings across 36 plant species in five different forests. Mean arthropod densities on control saplings ranged between 15 arthropods per square metre in LAK and 46 arthropods per square metre in TOM (Figure 2). The additive model, which incorporates both treatment and site, demonstrated the best performance in predicting total arthropod densities (X_2 = 79.62, df = 2, P < 0.001; X_2 = 14.72, df = 4, P = 0.005; Figure 2). The exclusion of birds led to a significant increase in mean arthropod density by 70 % in comparison to the control saplings (z = 7.89, P < 0.001) in all forest study sites. Similarly, in the absence of bats, arthropod density increased significantly by 65 % in comparison to the control saplings (z = 7.53, P < 0.001) (Figure 2).

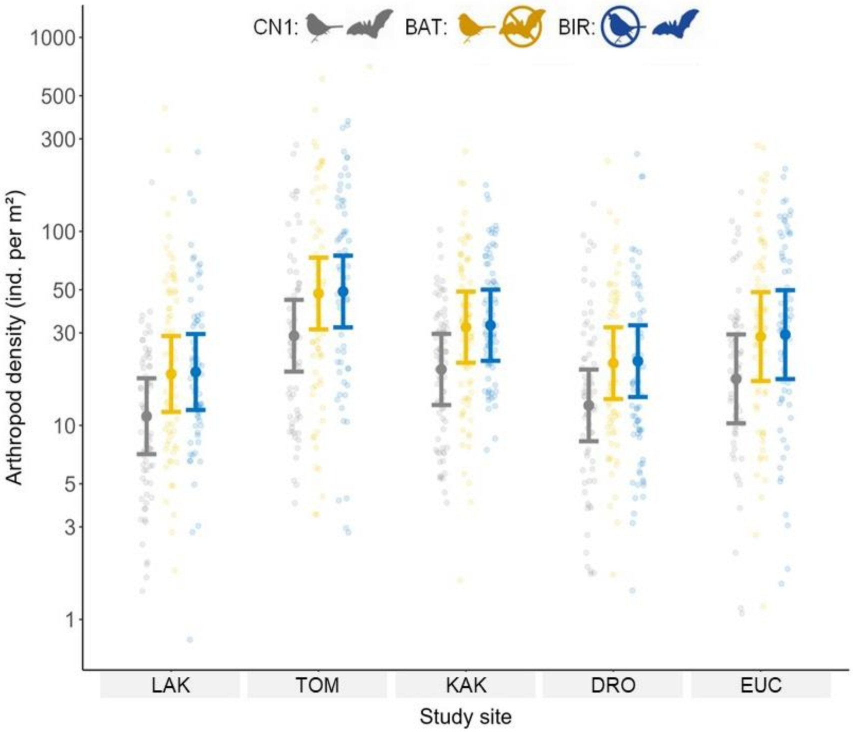

Figure 2: Effects of the exclusion of birds and bats on the total densities of all arthropods per square metre of foliage at each study site. Individual data point represents the density of arthropods on an individual sapling. The y-axis is on a log scale. Square and whiskers mark estimated marginal means and standard errors of the most parsimonious model (Table S1.3). Note that the study sites are arranged from left to right following their north-to-south latitudes. CN1 = control treatment, BAT = bat exclosure, BIR = bird exclosure.

Arthropod feeding guilds

Mesopredators were the most abundant feeding guild (7,233 individuals, 49 % of all arthropods), followed by sapsuckers (3,827 individuals; 26 %), NR arthropods (2,180; 15 %), and leaf chewers (1,543; 11 %). At the end of the experiment, after excluding birds in all study sites, mesopredators (z = 2.86, P = 0.01; Figure 3b), sapsuckers (z = 4.01, P < 0.001; Figure 3c) and NR arthropods (z = 4.32, P < 0.001; Figure 3d) had significant increases in densities —by 124%, 716%, and 1002%, respectively. However, despite detectable increases, especially in bat exclosures (i.e., + 146%; Figure 3a), changes in the densities of leaf chewers were not statistically significant (z = 1.77, P = 0.13).

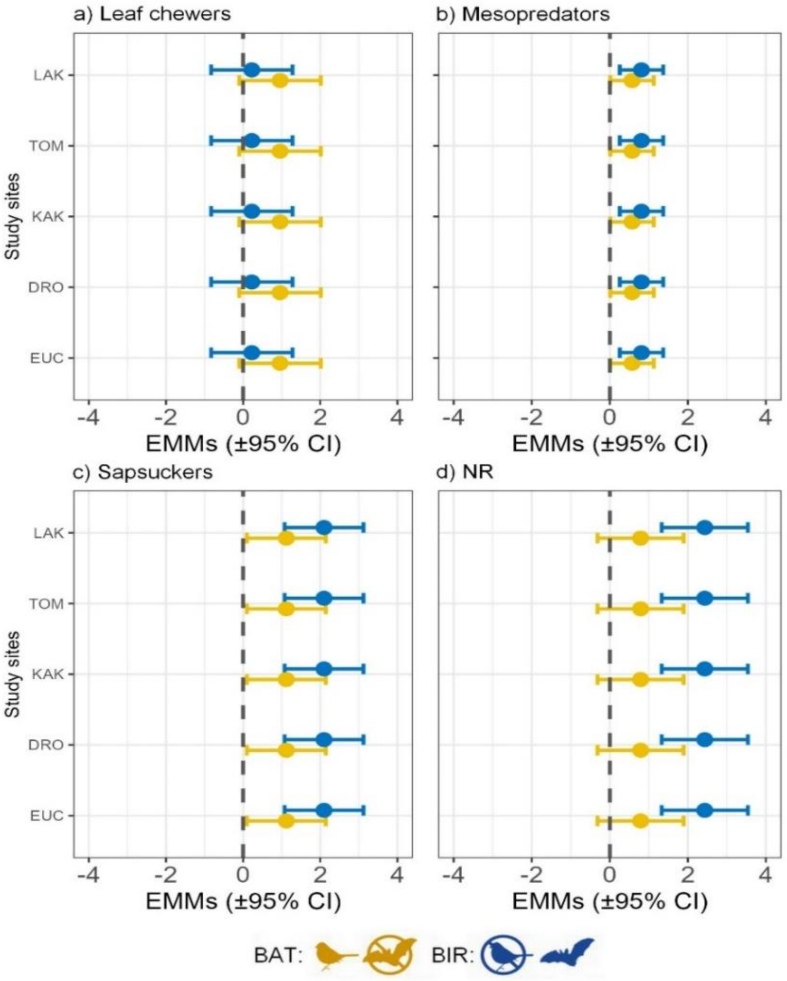

Figure 3: Caterpillar plot showing how the feeding guilds: leaf chewers (a), mesopredators (b), sapsuckers (c) and NR (d), respond to bat exclosure (BAT, yellow) and bird exclosure (BIR, blue) experiments. The X-axis shows the estimated marginal means (EMMs) of each treatment against the control (dashed line = no change from control) with a 95% confidence interval of the most parsimonious model including the variable treatment (Table S1.4). Values to the right of the dashed line indicate a positive effect, i.e., increased density of the guild in the predator

exclosure. When the confidence interval is strictly above the dashed line, the effect is significant ($P<0.05$). BAT = bat exclosure, BIR = bird exclosure.

Arthropod groups/orders

The most abundant arthropod group/order was Araneae (3,360 individuals), followed by Hymenoptera (3,178), Hemiptera (2,278), Coleoptera (1,102), Lepidoptera larvae (660) and Orthoptera (496). The exclusion of birds led to a significant increase of Hemiptera (z = 3.20, P = 0.004; Figure S1.1a) and Hymenoptera (z = 2.61, P = 0.02; Figure S1.1b) densities in all study sites and Orthoptera in KAK (z = 4.41, P < 0.001) and DRO (z = 3.73, P < 0.001; Figure S1.1e). In the absence of bats, only the Orthoptera density increased significantly in KAK (z = 2.69, P = 0.01; Figure S1.1e). None of the exclosures significantly changed the Coleoptera, Araneae and Lepidoptera larvae densities.

Change in herbivory damage

Overall, we found that the mean herbivory damage accumulated during the 1-month-long experiment on control saplings ranged from 0.1% in BUB to 6.7% in TOM (Figure 4). Bird and bat exclusions always led to an increased herbivory damage, but the magnitude of this effect varied between study sites (X_2 = 91.11, df = 10, P < 0.001, Table S1.3, Figure 4). Specifically, the exclusion of birds alone resulted in a significantly higher increase in mean herbivory damage by 87 % compared to the controls (z = 3.78, P < 0.001) in LAK. In contrast, both bird and bat exclusions led to a significant increase in mean herbivory damage compared to the controls in BUB (z = 7.22, P < 0.001, +500 %; z = 5.20, P < 0.001, +263 %; respectively), KAK (z = 2.53, P = 0.030, +51 %; z = 3.63, P < 0.001, +80 %), DRO (z = 6.28, P < 0.001, +198 %; z = 5.70, P < 0.001, +171 %), and EUC (z = 9.09, P < 0.001, +505 %; z = 9.42, P < 0.001, +541 %) (Figure 4).

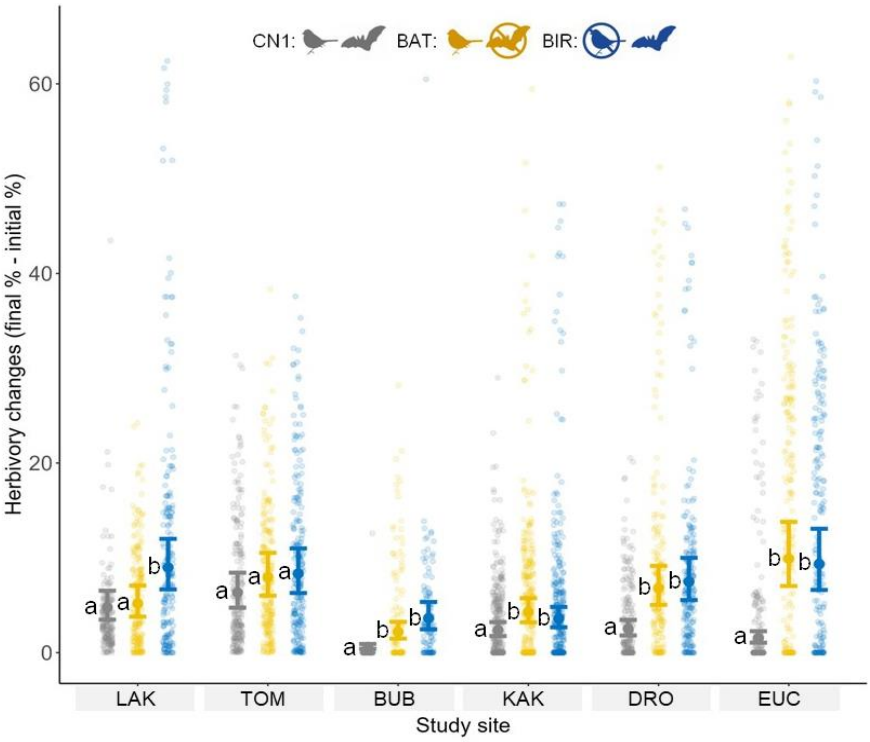

Figure 4: Effects of the exclusion of birds and bats on the herbivory damage of individual saplings at each study site. Individual data point represents the herbivory damage accumulated during the experiment on a twig from an individual sapling. Square and whiskers mark estimated marginal means and standard errors of the most parsimonious model (Table S1.3). Significant pairwise comparisons between predictors within a study site were tested by Tukey post hoc tests and are indicated with letters. Note that the study sites are arranged from left to right following their north-to-south latitudes. Eighteen extreme values of herbivory have been excluded for visualisation purposes but have not been omitted from the analysis. CN1 = control treatment, BAT = bat exclosure, BIR = bird exclosure.

Vertebrate predators

We observed greater diversity of birds and bats in tropical forest sites (BUB, KAK, DRO). There was no significant correlation between observed bird relative abundance and bird richness (R~-0.06). For instance, the tropical rainforest site, BUB, which boasted the highest species richness, paradoxically exhibited the lowest relative abundance of birds. The additive model incorporating both treatment and observed bird richness performed the best in predicting arthropod densities (X_2 = 5.14, df = 1, P = 0.02; X_2 = 57.93, df = 2, P < 0.001; Table S1.6). There was a consistent decrease in arthropod densities with increasing observed bird richness, but the difference between treatments remained constant (Figure 5a).

Both observed bird richness and relative abundance, in interaction with treatment, significantly impacted the mean herbivory accumulated during the experiment (X_2 = 28.64, df = 2, P < 0.001; X_2 = 10.29, df = 2, P = 0.005, respectively; Table S1.6). Herbivory damage decreased with increasing bird richness (Figure 5b), with a stronger reduction in controls compared to treatments. Bird relative abundance had the opposite effect on herbivory, with a stronger increase for the controls than the bird exclosures (Figure 5c).

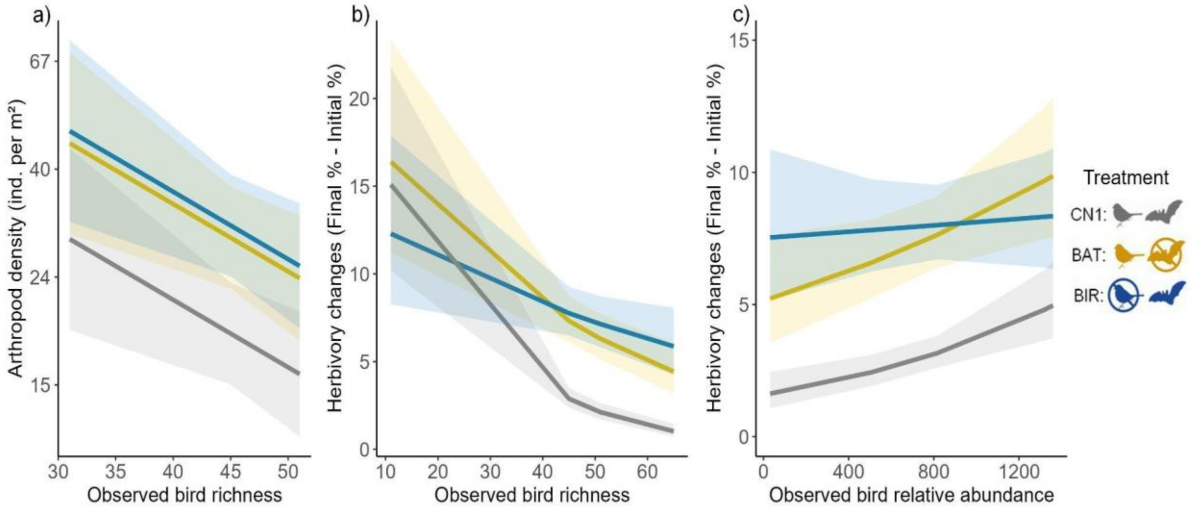

Figure 5: Correlations between the effect of treatments on arthropod densities and observed bird richness (a), on herbivory changes (mean final % - mean initial % of leaf area lost) and observed bird richness (b) and observed bird relative abundance (c). CN1 = control treatment, BAT = bat exclosure, BIR = bird exclosure.

When all study sites were included, the variations in arthropod density were not correlated with the expected richness of birds and bats. Only treatment showed a notable effect on arthropod densities (X_2 = 79.61, df = 2, P < 0.001, Table S1.7). However, the expected bat and bird richness in interaction with treatment, significantly affected the mean herbivory damage (X_2 = 30.50, df = 2, P < 0.001, Table S1.7). Once again, herbivory damage decreased with increasing bird richness, showing a steeper decrease in controls compared to treatments (Figure S1.2).

Discussion

The exclusion of birds and bats led to an increase in the density of all arthropods to the same extent across all study sites. Although we did not observe any significant effect on the density of leaf chewers, clear increases in herbivory damage were detected, particularly in warm temperate and tropical forests. Specifically, the exclusion effect on herbivory intensified with increasing vertebrate richness and decreased with increasing abundance of birds. Overall, our results suggest that top-down control of herbivory (i.e., the strength of the trophic cascade) is most pronounced in regions with greater diversity of vertebrate predators, aligning with our initial hypothesis. However, this pattern in the trophic cascades does not align with the consistent levels of predation (i.e., the direct impact of predators on arthropods) observed across all study sites. In the following discussion, we explore possible reasons for the observed deviations from theoretical expectations and suggest future research directions to improve our understanding of these dynamics.

Effects on arthropod densities

Despite we observed significant variations in arthropod densities between study sites, the absence of birds and bats had a surprisingly consistent and strong positive impact on arthropod densities across all study sites. Consequently, we did not find a correlation between the strength of the effects and the richness and abundance of vertebrate predators. It contradicts our assumptions and the widely accepted notion that biotic interactions are stronger at lower compared to higher latitudes (Schemske et al., 2009). Nevertheless, this aligns with an earlier meta-analysis (Borer et al., 2006) which emphasized that trophic cascade strength is primarily influenced by predator efficiency rather than species richness or system productivity. This finding is also supported by other meta-analyses that indicate no effect of latitude on vertebrate predation in forest understories (Mooney et al., 2010; Sam et al., 2022). The ability of individual predator species to maintain prey suppression at levels equal to or exceeding those of species-rich mixtures may be attributed to the "sampling effect" (Ives et al., 2005). This effect suggests that one dominant predator can have a strong influence, regardless of the number of coexisting predators (Griffin et al., 2013). Another explanation could be the functional redundancy within predator assemblages, indicating that a species-rich mixture may not necessarily outperform a less diverse one (Casula et al., 2006).

As another surprise with respect to our expectations, our current experiment did not reveal differences in the strength of predation between birds and bats. This is despite, prior studies have highlighted pronounced variations in arthropod regulation by these two predators (Kalka et al., 2008; Williams-Guillén et al., 2008). Specifically, Katka *et al.* (2008) demonstrated a stronger effect of bats than birds on arthropods. In contrast, Williams-Guillén *et al.* (2008) found a more significant impact of birds than bats on arthropods during the dry season, with the opposite trend observed in the wet season. However, when comparing trends among leaf chewers, mesopredators, sapsuckers, and NR arthropods, distinctions between the two types of exclosures in our experiment became evident. Significantly, only bird exclosures demonstrated effects on mesopredators, sapsuckers, and NR arthropods, while bat exclusion did not achieve significance in any of the feeding guilds.

Indeed, the absence of birds led to increased mesopredator and sapsucker densities while leaving leaf chewers significantly unaffected. In our study, mesopredators were represented by various groups, including Araneae, Hymenoptera, Coleoptera, and Orthoptera. Among them, only predatory Hymenopterans and Orthopterans increased their densities in bird exclosures.

Numerous bird species are known to feed on Hymenoptera (e.g., Mansor et al., 2018; Razeng & Watson, 2015; Sam et al., 2017) and Orthoptera (e.g., Joern, 1986; Poulin & Lefebvre, 1996) sometimes in substantial quantities (Nyffeler et al., 2018). The role of birds as intraguild predators also aligns with findings in other studies (Cassano et al., 2016; Gras et al., 2016; Maas et al., 2013; Ocampo-Ariza et al., 2023). The phenomenon, known as 'mesopredator release,' can have cascading effects on various arthropod groups: (a) The increase in mesopredators might have been robust enough to maintain a balance within the leaf chewer guild, resulting in minimal effects of birds on this particular group (Ferreira et al., 2023; Mooney et al., 2010). As a counterexample, despite not achieving statistical significance, bat exclusion resulted in a substantial increase in the densities of leaf chewers (+105%), while having no effect on mesopredators; (b) In the bird exclosures, we collected approximatively 800 ants (i.e., twice more than in controls) at the end of the experiment. This release of ants, classified as mesopredators, has the potential to enhance sapsucker densities. Indeed, ants occasionally have a strong and positive relationship with sapsucking insects, notably by providing protection against parasitoids and other predators (Styrsky & Eubanks, 2006; Wielgoss et al., 2014). We did not expect sapsuckers to be an important prey for birds, as they are largely sessile and small, which makes them less susceptible to predation. Yet, direct consumption of sapsuckers by birds has been documented in a recent tropical study (Ferreira et al., 2023). Thus, the significant increase in sapsucker densities observed in bird exclosures may be the result of a combination of both mutualisms with ants and no consumption by birds (of both ants and sapsuckers).

Effects on foliage herbivory and its correlation with vertebrate richness

Contrary to changes in arthropod density but in line with our initial assumptions, top-down control of herbivory is strongest in warm temperate and tropical forests, which are also the richest sites in terms of vertebrate species. Therefore, vertebrate predators were potentially more important in protecting plants from herbivory in warm temperate and tropical forests than in cold temperate forests. The disparity between arthropod and herbivory patterns can be attributed to the variability of palatability and defence traits of plants (Marquis et al., 2001; Poorter et al., 2004), as well as characteristics relating to their abundance and distribution (Terborgh, 2012) in the study sites. Indeed, effective plant defence mechanisms (Johnson et al., 2010), coupled with the low nutritional quality of food (Haukioja et al., 1991) in certain systems, as well as the impact of the abiotic environment (Castagneyrol et al., 2018; Huberty & Denno, 2004), may diminish the effectiveness and impact of herbivores. Another factor to consider is behaviourally mediated cascades, where the presence of predators can inhibit herbivore feeding, significantly lowering herbivory levels without necessarily affecting herbivore densities (Thaler & Griffin, 2008). It might be the case in our experiment where exclosures were relatively small, preventing direct access of predators to arthropods, yet still allowing them to fly around and potentially disrupt the feeding behaviour of the herbivores.

Unexpectedly, the observed effects show a negative correlation with the relative abundance of birds. This implies that having higher numbers of vertebrate predators does not necessarily translate to improved predation efficiency. Nevertheless, our results should be interpreted with caution, as point counts do not directly infer bird absolute abundance and bat abundance was entirely overlooked. Indeed, bird detectability differs significantly between the understory of a tropical rainforest and a temperate forest. While more open spaces would favour visual detections, the observer avoidance effects demonstrated in other studies (Darras et al., 2018; Fernández-Juricic et al., 2001) indicate that abundance estimations from point count data are likely biased (Hayes & Monfils, 2015).

Overall, among study sites, the levels of defoliation accumulated over the experiment reached a maximum average of 19% of leaf area lost in the absence of vertebrate predators. This could potentially reduce the overall growth or reproductive output of saplings (Wang et al., 2021) and may also to a lesser degree, result in mortality (Núñez-Farfán & Dirzo, 1991), especially combined with other factors such as resource depletion (Landhäusser & Lieffers, 2012) or water deficiency (Gerhardt, 1998). Furthermore, defoliation caused by arthropods can make plants more susceptible to diseases (Nakazawa et al., 2012), as arthropods are common vectors of plant pathogens (viruses, bacteria, and fungi) (Eigenbrode et al., 2018; Nault, 1997). Previous research suggests that bats, by reducing insect populations, lower the occurrence of insect-borne pathogens (Maine & Boyles, 2015). Therefore, we could speculate that the absence of vertebrate predators, leading up to 5 times higher accumulation of herbivory damage, may have disastrous consequences on sapling survival, potentially altering forest dynamics.

Caveats and prospects

Consideration of limitations in our methodology is also crucial when interpreting the disparity between the observed patterns in arthropod density and herbivory. Herbivory accumulated throughout the entire duration of the experiment, whereas arthropods were collected at a specific time, and are highly influenced by various factors such as temperature, humidity, and the time of collection. As emphasized by Sivault *et al.* (2023), annual breeding cycles, and thus peaks in their abundances, of arthropod herbivores must be considered. It is plausible that the collection time occurred after the peak of caterpillar or sawfly larvae abundances (i.e., primary leaf chewers in our study). It may have resulted in smaller effects of exclosures on overall leaf chewers. To address this caveat, a different approach could involve accounting for temporal variation (e.g., seasonal effects, migrations, annual breeding cycles) in the predator exclosure experiments (Schmitt et al., 2021; Van Bael et al., 2003; Williams-Guillén et al., 2008).

Considering the distinct activity patterns of birds and bats throughout the day, one might anticipate their effects to be additive, implying stronger trophic cascades when they are present together (Morrison & Lindell, 2012; Williams-Guillén et al., 2008). However, a consistent observation of this phenomenon is lacking; in some instances, the effects of bats and birds appeared not additive (i.e., exhibiting the same effect together or alone) or even slightly antagonistic (i.e., lower together than alone) (Ocampo-Ariza et al., 2023; Sivault et al., 2023). Future directions could involve establishing permanent exclosures to determine whether the strength of bird and bat predation has an additive effect and if it varies between locations (Cassano et al., 2016; Karp & Daily, 2014; Maas et al., 2013; Ocampo-Ariza et al., 2023). Currently, we lack information on the extent to which the diets of sympatric birds and bats overlap, and whether the two groups are functionally redundant. For such considerations, it is important to note that they likely feed on different stages of arthropod herbivores. For example, while bats hunt adult moths, their impact on the densities of chewing arthropods may be stronger but postponed compared to birds feeding on individual caterpillars. Additional approaches should be employed to better assess the relative contribution of birds and bats to predation levels such as diet DNA metabarcoding and quantification of the amount of prey items consumed (Aizpurua et al., 2018; Garfinkel et al., 2022), coupled with species-specific surveys involving passive acoustic and capture methods.

Conclusion

The functional significance of birds and bats was demonstrated in our study by effectively reducing arthropod densities and causing significant declines in herbivory damage. However, while the effect of predator exclosure on arthropod densities remained consistent across study sites, effects of predator exclusions on herbivory damage intensified from cold to warm temperate and tropical forests, aligning with the richness of vertebrate predators. This discrepancy highlights the need for further research into the importance of bottom-up effects within our respective study sites. Nevertheless, these robust effects were obtained only after a one-month-long experiment, and one could anticipate an even more pronounced impact over an extended period. In summary, conducting a standardized empirical study on the impact of birds and bats in the top-down regulation of herbivores on a broad geographical scale poses methodological challenges. Nevertheless, such a study establishes baseline data for predicting the impacts of environmental changes on ecosystem services pertinent to forest primary productivity.

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Author contributions

ES, JK, MHT, AJP, XX, SF, SFG, HM, JL, ML, MW and KS conducted the fieldwork and collected the data, MW led the arthropod sorting and identification, KS, HM, TV, JJL led the leaf herbivory analysis with the support of several undergraduate students, ES performed the data analyses, LRJ helped with the analyses, KS designed and funded the study, ES wrote the first draft of the manuscript and all co-authors contributed significantly to revisions.

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Supporting information

Appendix S1

Table S1.1: Plant species used for the experiment at each study site (LAK, TOM, BUB, KAK, DRO, EUC) and during each sampling year.

	LAK	TOM		BUB	KAK		DRO		EUC	
	2022	2018	2019	2019	2020	2021	2018	2019	2018	2019
Tilia cordata	X									
Acer pseudoplatanus	X									
Fraxinus excelsior	X									
Acer platanoides	X									
Quercus robur	X									
Carpinus betulus	X									
Ulmus glabra	X									
Magnolia kobus		X	X							
Syringa reticulata		X	X							
Carpinus cordata		X	X							
Acer mono		X	X							
Prunus ssiori		X	X							
Acer palmatum		X	X							
Fraxinus lanuginosa		X	X							
Betula maximowiczia		X	X							
Garcinia cowa				X						
Diospyros kaki				X						
Orophea laui				X						
Cleidion brevipetiolatum				X						
Shorea wangtianshuea				X						
Baccaurea ramiflora				X						

Pittosporopsis kerrii				X						
Saprosma ternata				X						
Pometia pinnata					X	X				
Pimelodendron amboinicum					X	X				
Dysoxylum arborescens					X	X				
Erythrospermum candidum					X	X				
Chrysophyllum roxburghii					X	X				
Celtis latifolia					X	X				
Gymnacranthera paniculata					X	X				
Ficus erythrosperma					X	X				
Cleisthanthus myrianthus							X	X		
Cryptocarya sp.							X			
Haplostichanthus ramiflorus							X	X		
Myristica globosa							X	X		
Rockinghamia angustifolia							X	X		
Endiandra leptodendron							X	X		
Argydendron peralatum							X	X		
Dysoxylum sp.								X		
Bursaria spinosa									X	X
Acacia parramattensis									X	X
Eucalyptus tereticornis									X	X
Breynia oblingifolia									X	X
Eucalyptus pruinosa									X	X

Table S1.2: Starting and ending times of the experiment at each study site (LAK, TOM, BUB, KAK, DRO, EUC) and during each sampling year.

	YEAR	START	END
LAK	2022	13/04	16/05
TOM	2018	20/05	19/05
	2019	12/05	11/06
BUB	2019	24/08	19/09
KAK	2020	30/08	29/09
	2021	01/10	31/10
DRO	2018	05/11	10/12
	2019	25/10	30/11
EUC	2018	05/11	10/12
	2019	26/10	24/11

Table S1.3: Comparisons of multi-predictor models analysing factors (i.e., treatment and site) affecting the density of all arthropods. Results of the analysis of deviance based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in grey.

	Arthropod densities		Herbivory damage	
	dAICc	df	dAICc	df
Null	76.8	4	243.0	5
Treatment	4.2	6	107.1	7
Site	72.6	8	203.5	10
Treatment + Site	**0.0**	**10**	67.9	12
Treatment * Site	9.1	18	**0.0**	**22**

Table S1.4: Comparisons of multi-predictor models analysing factors (i.e., treatment and site) affecting the density of leaf chewers, predators, sapsuckers, and NR, based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in grey.

	Chewer densities		Predator densities		Sapsucker densities		NR densities	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Null	17.6	4	16.0	4	62.4	4	30.4	4
Treatment	18.2	6	11.5	6	50.3	6	15.2	6
Site	**0.0**	**8**	4.5	8	12.0	8	16.5	8
Treatment + Site	0.6	10	**0.0**	**10**	**0.0**	**10**	**1.2**	**10**
Treatment* Site	7.0	18	12.2	18	14.2	18	0.0	18

Table S1.5: Comparisons of multi-predictor models analysing factors (i.e., treatment and site) affecting the density of Hemiptera, Hymenoptera, Coleoptera, Orthoptera, Araneae and Lepidoptera larvae, based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in grey.

	Hemiptera densities		Hymenoptera densities		Coleoptera densities		Orthoptera densities	
	dAICc	df	dAICc	df	dAICc	df	dAICc	df
Null	14.1	4	48.6	4	17.5	4	81.4	4
Treatment	5.8	6	45.6	6	16.5	6	71.4	6
Site	8.3	8	2.8	8	1.9	8	15.8	8
Treatment + Site	**0.0**	**10**	**0.0**	**10**	**0.9**	**10**	5.9	10
Treatment* Site	8.3	18	5.5	18	0.0	18	**0.0**	**18**

	Araneae densities		Lepidoptera larvae densities	
	dAICc	df	dAICc	df
Null	15.7	4	44.7	4
Treatment	19.7	6	44.2	6
Site	**0.0**	**8**	0.5	8
Treatment + Site	4.1	10	**0.0**	**10**
Treatment* Site	11.6	18	3.2	18

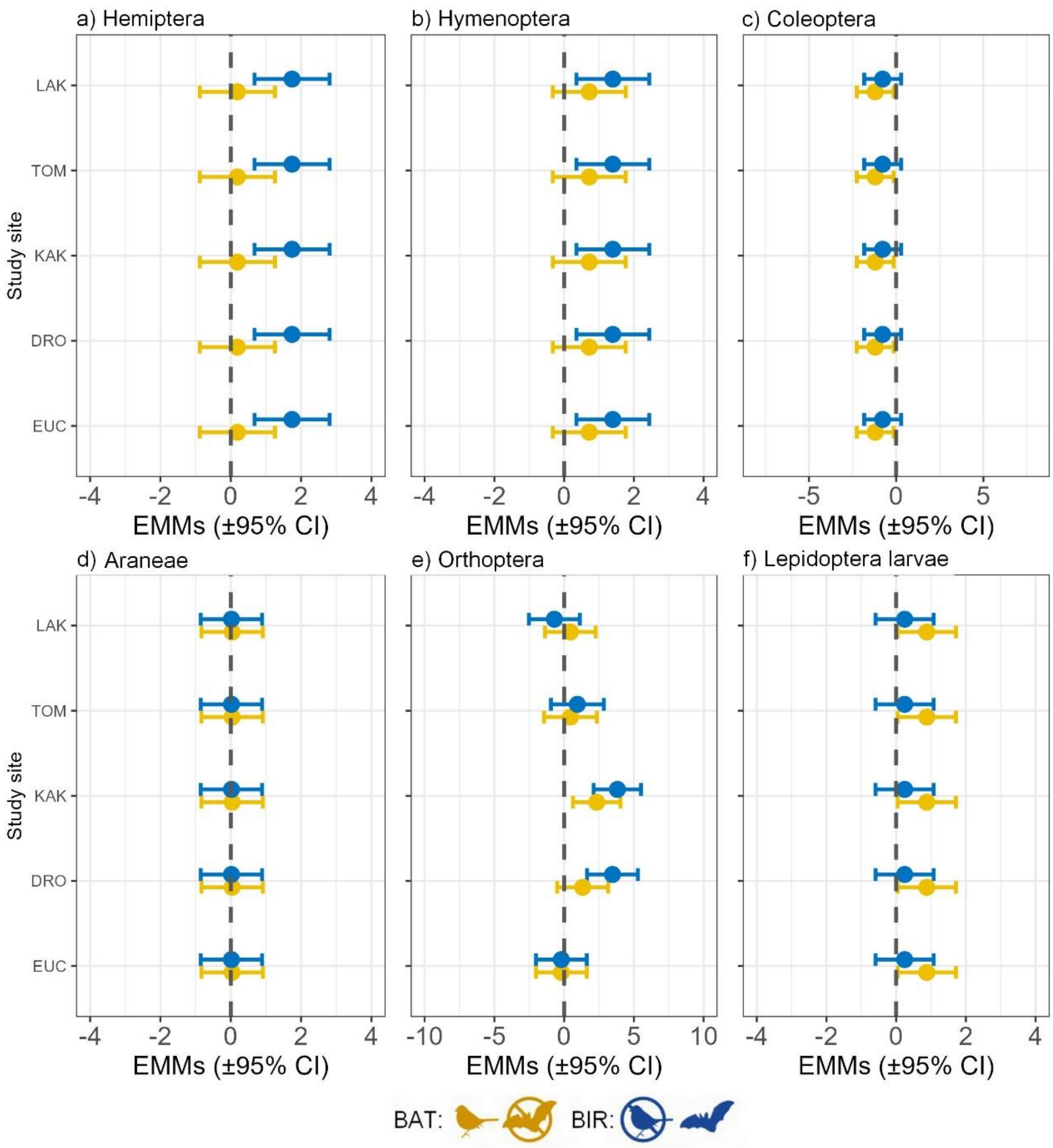

Figure S1.1: Caterpillar plot showing how the arthropod orders (Hemiptera (a), Hymenoptera (b), Coleoptera (c), Araneae (d), Orthoptera (e) and Lepidoptera larvae (f)) respond to bat (BAT, yellow) and bird (BIR, blue) exclusion experiments. The X-axis shows the estimated marginal means (EMMs) of each treatment against the control (dashed line = no change from control) with a 95% confidence interval of the most parsimonious model including the variable treatment (Table S4). When the confidence interval is strictly above or below the dashed line, the effect is significant ($P<0.05$).

Table S1.6: Comparisons of multi-predictor models analysing factors (i.e., treatment, observed bird abundance, observed bird richness) affecting the density of all arthropods. Results of the analysis of deviance based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in grey.

	Arthropod densities		Herbivory damage	
	dAICc	df	dAICc	df
Null	54.2	5	160.7	6
Observed bird richness	51.9	6	156.0	7
Observed bird abundance	53.3	6	162.6	7
Treatment	2.3	7	31.8	8
Observed bird richness + Observed bird abundance	53.9	7	153.0	8
Treatment + Observed bird richness	**0.0**	**8**	27.1	9
Treatment + Observed bird abundance	1.4	8	33.6	9
Treatment + Observed bird richness + Observed bird abundance	2.0	9	24.2	10
Treatment* Observed bird richness	2.8	10	9.2	11
Treatment* Observed bird abundance	4.4	10	33.9	11
Treatment + Observed bird richness + Observed bird abundance + Treatment:Observed bird richness	4.9	11	6.3	12
Treatment + Observed bird richness + Observed bird abundance + Treatment:Observed bird abundance	5.0	11	24.4	12
Treatment + Observed bird richness + Observed bird abundance + Treatment:Observed bird richness + Treatment:Observed bird abundance	8.8	13	**0.0**	**14**

Table S1.7: Comparisons of multi-predictor models analysing factors (i.e., treatment and expected bird and bat richness) affecting the density of all arthropods. Results of the analysis of deviance based on the delta AICc (Corrected Akaike Information Criterion). The most parsimonious models are indicated in grey.

	Arthropod densities		Herbivory damage	
	dAICc	df	dAICc	df
Null	72.6	5	170.5	6
Treatment	**0.0**	**7**	34.6	8
I(Expected bird richness + bat richness)	74.3	6	162.2	7
Treatment + I(Expected bird richness + bat richness)	1.7	8	26.4	9
Treatment*I(Expected bird richness + bat richness)	1.8	10	**0.0**	**11**

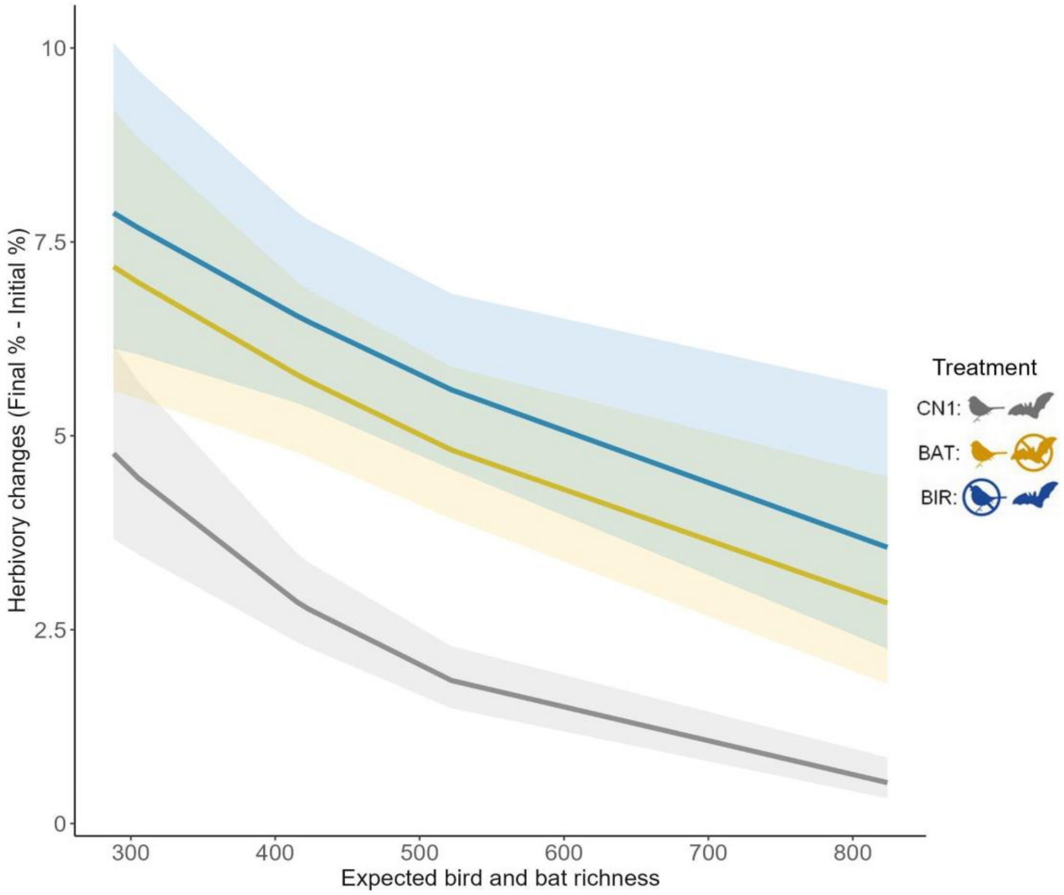

Figure S1.2: Correlations between the effect of treatments on herbivory changes (mean final % - mean initial % of leaf area lost) and expected bird and bat richness (obtained from public databases). CN1 = control treatment, BAT = bat exclosure, BIR = bird exclosure.

3. Conclusion and future prospects

My thesis aimed to describe the top-down regulation of arthropods and its indirect impact on herbivory across different spatial scales, highlighting the role of bats as predators of arthropods.

In **Chapter 1**, employing a multi-method approach, we conducted a survey of bats along an elevational transect in Papua New Guinea (PNG). In total, we found that Mt. Wilhelm hosts at least one-third of the bat species richness expected in that region. In line with our expectations, bat species richness exhibited a decrease with increasing elevation, primarily influenced by mean daily temperature. Species turnover characterized the distribution of species along the transect, while both turnover and nestedness were observed in the regional data. Notably, some bat species were exclusively detected at high elevations, beyond their historical range. As such, this study was the first detailed bat survey along an elevational forest transect on an island characterized by data deficiency and a limited understanding of bat assemblages and their ecological roles. Additionally, it underscored how the results of basic inventory surveys can raise important ecological questions and emphasize the necessity for comprehensive bat studies in PNG.

In **Chapter 2**, we tested whether flying vertebrates (birds and bats) and/or ants were suppressing arthropods effectively and investigated whether their predation pressure cascaded down to plants to a consistent degree across seasons and elevations. Employing two six-month-long predator exclusion experiments, we restricted access of flying vertebrates and ants (both individually and in combination) to saplings along the same elevational transect as described in Chapter 1. Our findings revealed that the absence of flying vertebrates led to a significant increase in the density of arthropods, averaging a 37% rise, particularly among large arthropods. Simultaneously, plant herbivory showed an average increase of 50%. Overall, the absence of ants did not exhibit significant effects. These patterns remain strong across the entire transect but the magnitude of the effects was generally site-specific and much higher during the wet than dry season. We also demonstrated that predation risk on arthropods correlated with the abundance of predatory birds, with less significance observed for bats. In summary, this study highlighted the substantial impact of flying vertebrates, as opposed to ants in top-down control of herbivory, across seasons and elevations. Considering this elevational transect as a proxy for the productivity gradient, where lowlands represent the wettest and warmest sites, we can anticipate an increase in herbivory damage with the global temperature rise but a decrease if precipitation declines. Yet, our findings are specific to the experiment's location, and a comprehensive understanding of these dynamics would require studying multiple mountains.

In **Chapter 3**, we examined whether bats and/or birds were responsible for the patterns described in Chapter 2, employing diurnal and nocturnal exclosures at four different elevations of the same elevational gradient. Our results revealed that bird exclusion led to a 31 % increase in arthropod densities, encompassing leaf chewers and mesopredators, irrespective of elevation. The effect of bats was detectable (+ 15 %), yet it did not reach statistical significance. However, both bird and bat exclusions effectively increased herbivory damage (up to 189 % more herbivory), a trend observed exclusively in the highlands (~ 2,200-2,700m asl). Establishing a direct link between arthropod densities, herbivory damage, and vertebrate predators proved challenging, likely due to methodological limitations. Consequently, our study offered several recommendations for herbivory measures and arthropod collection in future research. Nonetheless, it marked the first attempt to exclude birds and bats separately and simultaneously at multiple elevations, revealing a site-specific contribution of birds and bats in limiting foliage herbivory on young trees.

In **Chapter 4**, using a canopy crane and improved methods based on earlier observations from Chapters 2 and 3, we conducted predator exclusion experiments in the canopy and understory of a temperate forest. Like Chapter 2, despite focusing on a completely different system, our study demonstrated that flying vertebrates, but not ants, play a crucial role in reducing arthropods (by 81 %) in both the forest canopy and understory. This reduction results in a significant decrease of 42 % in plant damage. Furthermore, birds and bats individually contribute to significant decreases in arthropod densities (by 89 and 63 %, respectively), and reductions in herbivory damage (by 28 and 22 %) in the forest understory. Birds, bats, and ants appeared to exhibit antagonistic relationships in influencing arthropod density but additive relationships in herbivory damage. It underscores once again the methodological challenge of establishing a connection between arthropod and herbivory changes (Chapter 3). Nevertheless, our findings confirmed previous hypotheses suggesting that vertebrates exert a more influential role in top-down control compared to ants, a pattern likely extending to various other ecosystems (e.g., Chapter 2). Furthermore, it emphasized that vertebrates play a consistent role in preserving ecological balance across different layers of a single forest.

In **Chapter 5**, assuming that vertebrates are largely responsible for top-down forces worldwide, we focused solely on the individual effect of birds and bats on arthropod densities and herbivory damage in forests of different latitudes. As observed in my previous chapters, the exclusion of birds and bats consistently led to an increase in the density of all arthropods by 70 % across study sites. Although no impact was observed on the density of leaf chewers, significant variations in herbivory damage (up to 500 % more herbivory) were detected, especially in the warm temperate and tropical forests. In summary, in contrast to the effect of exclusions on arthropods, our findings on herbivory damage align with our expectations, demonstrating a stronger top-down control of herbivory in warm temperate and tropical regions compared to cold temperate regions. This positively correlated with the richness of vertebrate predators. Obtaining such robust effects over a one-month-long experiment, which we conducted, underscores once more the crucial role of birds and bats as predators of arthropods in forest ecosystems. The observed discrepancy between top-down control of arthropods and herbivory highlights the necessity for further research into the bottom-up influences on these patterns. Hence, the efficiency and replicability of this study provide a baseline for future research exploring broad-scale variations in trophic cascades.

In summary, the key conclusion drawn from the presented chapters underscores the importance of recognising bats as key predators influencing top-down forces in forest ecosystems. Indeed, my chapters revealed relatively comparable effects of birds and bats on arthropods, and indirectly on herbivory (Figure 1). Notably, the findings indicated that excluding both birds and bats led to significant increases—ranging from half to nearly double—in the density of arthropods on foliage. This pattern remained consistent across different elevations, strata, and latitudes. In contrast, top-down control of herbivory exhibited substantial variation between locations (Figure 1), increasing with rising richness of birds and bats. Overall, my findings underscore the complexity and interconnected nature of relationships across different trophic levels, thereby emphasizing the necessity for research on the contribution of bottom-up control to these effects.

Indeed, while significant progress has been made in comprehending multitrophic interactions over the past few decades, it is essential to recognize that our current understanding represents only the tip of the iceberg. The rapid development of this field, driven by specific-group exclusion experiments in recent years (Bhalla et al., 2023; Bouarakia et al., 2023; Ocampo-Ariza et al., 2023), is very promising. Nevertheless, the focus remained on the agricultural context because of the threat posed by herbivorous insects to agricultural commodities (Tuneu-Corral et al., 2023). Unlike the existing literature, my thesis delved into the top-down control in undisturbed forests, demonstrating that altering trophic cascades in these natural ecosystems could also yield disastrous consequences and thereby should not be overlooked. Furthermore, it is noteworthy that many of my research projects were conducted in the Australasian realm, filling a significant gap in existing literature, which primarily focused on the Palearctic and Neotropical realms (Maas et al., 2016; Ramírez-Fráncel et al., 2022).

Particularly, my thesis contributes novel insights into the understudied island of Papua New Guinea. To deepen our understanding, future studies must integrate into these experiments more robust acoustic surveys, which should be more spatially linked to the individual exclosures, and metabarcoding diet analysis of bird and bat insectivorous species occurring at the experimental sites (Blažek et al., 2021; Mata et al., 2019). The studies should also consistently account for temporal variations such as seasons, migrations, and breeding cycles both of prey and predators (Philpott et al., 2004; Van Bael et al., 2003; Williams-Guillén et al., 2008). Despite encountering methodological limitations throughout this thesis, I addressed most of them, ensuring the efficiency and replicability of my work. Consequently, my thesis opens avenues for further research in other mountainous regions and diverse geographic areas.

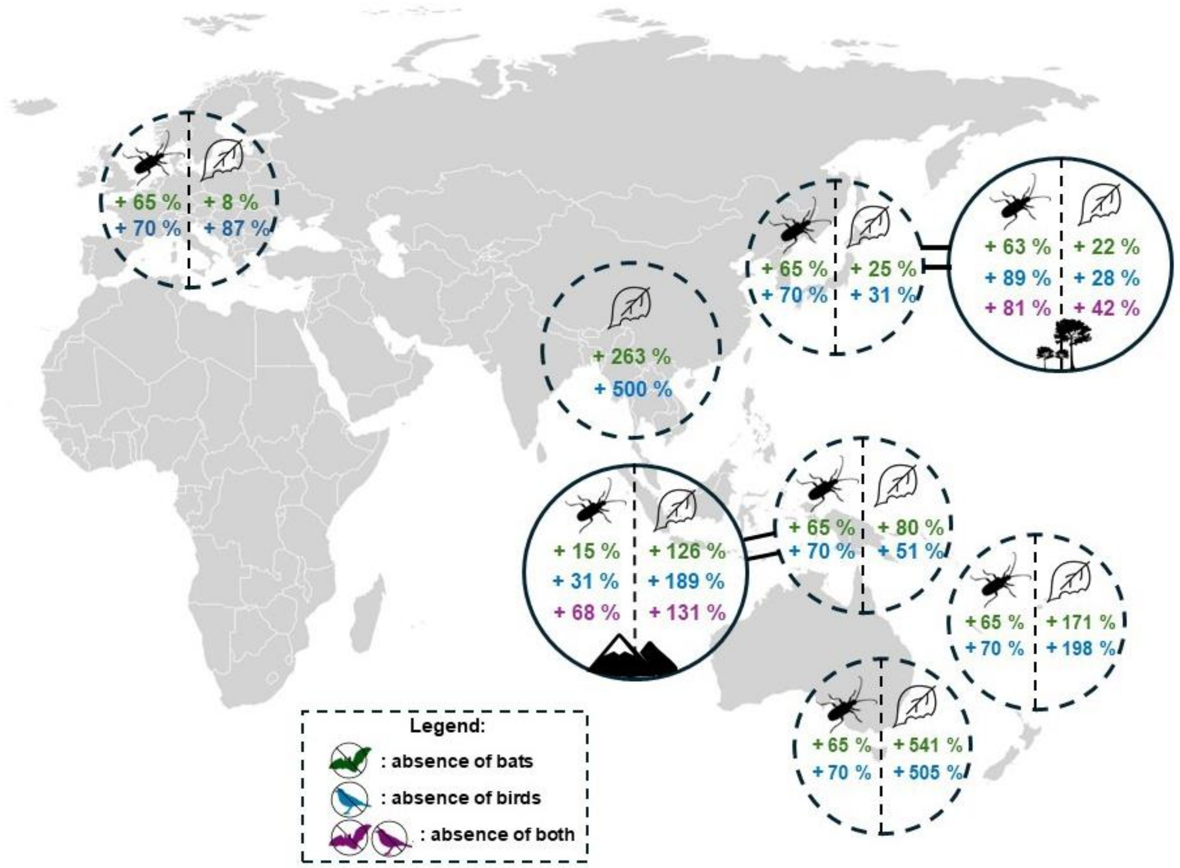

Figure 1: Summary map illustrating the overall impact of the absence of bats (green), birds (blue), and both birds and bats (purple) on arthropod densities (percentages beneath the

arthropod icon) and herbivory damage (percentages beneath the leaf icon) at each study location of the thesis. The use of plain circles and dashed circles differentiates between locations where permanent and group-specific exclusion experiments (plain circles) were conducted, and those where only group-specific exclusion (dashed circle) experiments were implemented. The percentages provided for the projects including several locations (i.e. elevational transect or vertical strata) represent the most significant effects observed across all elevations.

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4. Curriculum vitae

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EDUCATION

2019-ongoing:	**Ph.D. degree** at the University of South Bohemia (Czech Republic), specialization zoology. Supervisor: Katerina Sam Thesis: Roles of bats in top-down forces across elevations, strata, and latitudes.
2017-2019:	**MSc. Degree** at the Natural History Museum of Paris (France), specialization biodiversity, ecology, and evolution. Supervisors: Anthony Herrel and Pierre-Michel Forget. Thesis: Ecological, morphological, and evolutionary study of the mutualistic relationship between mammals and tropical forests.
2014-2017:	**BSc. Degree** at the University of Bordeaux (France) specialization ecology.

EMPLOYMENT

2019-ongoing:	Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ph.D. candidate.

INTERNSHIPS

August-October 2022:	Assessment of bat diversity and establishment of exclosure experiments in cacao plantations from the San Martin region, Peru. In cooperation with Dr. Teja Tscharntke and Dr. Ocampo-Ariza from the Georg-August-University, Germany.
November 2021:	Study of the bat intestinal microbiome in relation to the host genome in diet evolution. In collaboration with Dr. Ingala (National Museum of Natural History; NMNH), Washington DC (re-scheduled online due to covid-19 restrictions).
October 2019:	Assessment of bat diversity in Daintree Research Observatory with Dr. Krockenberger, from the James Cook University, Cairns, Australia.

PUBLICATIONS / H index 2 ; 7 citations ; 3 papers ; https://orcid.org/0000-0001-8970-1804

Sam, K., Re Jorge, L., Koane, B., Amick, P., **Sivault, E.** (2023) Vertebrates but not ants protect rainforest trees from herbivorous insects along an elevational gradient in Papua New Guinea. *Journal of biogeography, 50,* 1803-1816.

Sivault, E., Mc Conkey, K.R., Bretagnolle, F., Sengupta, A., Lambert, J., Heymann, E.W., Herrel, A., Forget, P.-M. (2023). Can body mass and skull morphology predict seed and fruit ingestion potential for mammal species? A test using extant species and its application to extinct species. *Functional ecology, 37*, 1504-1515.

Sivault, E., Amick, P. K., Armstrong, K. N., Novotny, V., & Sam, K. (2022). Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. *Biotropica, 55,* 81-94.

INTERNATIONAL CONFERENCES

12-16 February 2024: **European Conference of Tropical Ecology**: Sivault E., Fernández Garzon S., Finnie S., … , and Sam K. Bats and birds top-down regulate arthropods to a similar magnitude across temperate and tropical forests, Lisbon, Portugal. Oral presentation and poster.

19-23 June 2023: **Chair of the symposium** "Challenges in measuring mammal diversity in the tropics", and part of the **organizing committee** of the 6th **European conference of tropical ecology,** Ceske Budejovice, Czech Republic. Oral presentation.

7-9 June 2022: **European Conference of Tropical Ecology**: Sivault E., Amick P.K., Novotny V., Sam K. Species richness and community structure of bats along a forest elevational gradient in Papua New Guinea, Montpellier, France. Oral presentation.

10-14 August 2021: **1st Pacific Islands Bat Forum**: Sivault E., Amick P.K., Novotny V., Sam K. Species richness and community structure of bats along a forest elevational gradient in Papua New Guinea, online. Poster.

2-6 March 2020: **7th Frugivores and Seed Dispersal Symposium**: Sivault E., McConkey K.R., Bretagnolle F., Sengupta A., Lambert J., Heymann E., Forget P.-M., Herrel A. Body mass and skull dimensions predict seed dispersal capacity of bats, primates and carnivores from tropical forests, Corbett landscape, India. Oral presentation.

GRANTS & AWARDS

Travel grants:

- **IBERA Biology Centre Travel Grant** program 2021
- **IBERA Biology Centre Travel Grant** program 2022
- **ERASMUS + mobility project** 2022

Research grants:

- **Bat conservation international scholarship** (2023) with two special recognitions: Thomas H. Kunz Innovation in Bat Research Honor and Equitable Conservation award. (PI: 4,000 USD)
- **Bat Biology Foundation Grant program** (2023), Expedition and Fieldwork Grant program. (PI: 5,000 USD)

Awards:

- **2nd best student presentation** on Conference of PhD students of the department of Zoology, Faculty of Science, University of South Bohemia, 2023
- **1st PhD student at the Central European Final** of the Francophone contest **"My thesis in 180 seconds"** (MT180) and international final in Paris 2021. https://www.youtube.com/watch?v=kkdpt566GTY&ab_channel=Math%C3%A8seen180secondes-MT180

OTHER SCIENTIFIC EXPERIENCES

Co-author of the book: "PNG community conservation, guidebook for community conservation and biodiversity monitoring", Wildlife Conservation Society.
3 regular reviews for scientific journals
Coordinator of audio recording and camera trapping in LIFEPLAN Global Project