

Jihočeská univerzita v Českých Budějovicích

Přírodovědecká fakulta



The dynamics of trophic interactions: Predators, prey, plants and their interactions and communication in terrestrial ecosystems

Habilitation thesis

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2025

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Acknowledgements

I would like to extend my heartfelt gratitude to all current and former team members for their unwavering commitment, enthusiasm for science, and the vibrant, stimulating discussions that have enriched our shared journey. Your dedication has created a warm and inspiring working environment, where writing together and dreaming about grant proposals and projects became not only productive but genuinely enjoyable. This year's team, in particular, has been nothing short of extraordinary - surpassing even my wildest dreams. Your incredible support has significantly fuelled my motivation and even gifted me the precious time needed to complete this thesis. Your craziness, just little bit smaller than mine, kept me smiling through most of the working days.

I am deeply indebted to my mentors, whose guidance, wisdom, and encouragement have profoundly shaped my academic journey. I am equally grateful to the broader academic community for its collective passion for discovery. To the authors whose works have illuminated my path and the peers who have offered their insights and constructive critiques, thank you for reminding me that scientific progress is a shared endeavor, standing on the shoulders of giants. To my collaborators, board members of the societies in which I actively participate, and colleagues from around the world - thank you for broadening my horizons and enriching my scientific perspective. Your encouragement and fruitful collaborations have not only shaped my research but also made its scope delightfully diverse.

I am profoundly grateful to the European Research Council, the Grant Agency of the Czech Republic, the Biology Centre of the Czech Academy of Sciences, and the University of South Bohemia. These funding bodies and institutions have provided the resources, supportive environment, and opportunities that were crucial for this work. To the administrative and technical staff - your tireless efforts and kindness have made even the most challenging days more manageable, and for that, I am deeply appreciative (as more than anything else on this world, I hate financial reports).

Finally, my deepest thanks go to my husband, whose gentle encouragement have been my constant source of strength. Your promise of a new horse if I submitted this thesis was, without doubt, a clever and motivating touch! Last but certainly not least, I want to thank my children, whose unyielding curiosity and adventurous spirits brighten every grant-writing session and conference trip with the ever-enthusiastic question: "Where do we go next, mum?"

A summary of my research to date

I first became interested in the topic of predators and predation as a bachelor student of Roman Fuchs. Back then, I studied how small birds recognise their predators, kestrels and hawks, and how they behave near them at a feeding site when they are exposed to harsh winter conditions. I also changed the position of the predators and split them in half to see if the birds were able to use amodal completion, and still perceive them as dangerous objects (Tvardikova and Fuchs 2010, 2011, 2012). Later, towards the end of the master's programme, I was introduced to tropical forests (Sam et al. 2014) and entomology and suddenly immersed in a whole new world of predator-prey interactions and different patterns along elevational gradients (Tvardikova 2013, Colwell et al. 2016). The world of tropical forests, from which migratory birds fly thousands of kilometres just to escape high predation pressure, and where all trophic interactions, including predation, are expected to be intensified, especially in the lowlands. My scientific path meandered back and forth between avian ecology, community ecology, avian diet and prey intake and bird-insect interactions, ending up with multitrophic interactions, i.e., tritrophic interactions between plants, arthropods and invertivorous predators. After completing my successful postdoctoral project in Papua New Guinea and a postdoctoral stay in Australia at Griffith University and Queensland University, where I worked on various topics (Low et al. 2014, Wilson et al. 2016, Clark et al. 2018), I decided to return to the Czech Republic as a group leader. A year later, I secured funding from the Grant Agency of Czech Republic to expand my postdoctoral project for my lab and another two years later I even expanded the idea to a global experiment funded by the European Research Council Starting Grant.

My lab now focuses on different arthropod-feeding predators (referred to as insectivores hereafter, although technically invertivores), their feeding ecology and strategies, and their effects on lower trophic levels. Another important area of my research focuses on (i) communication between predators, prey and primary producers – mainly on olfaction in birds, on (ii) the indirect (non-lethal) effects of predation (Kollross et al. 2022) and (iii) how the gut microbiome is affected by the diet of predators (Bodawatta et al. 2018, Bodawatta et al. 2020a, Bodawatta et al. 2020b, Bodawatta et al. 2021a, Bodawatta et al. 2021b, Diez-Méndez et al. 2023). This last topic is not covered in this thesis as it is of little relevance to the other currently included topics. I conduct my research at different spatial scales, ranging from behavioural experiments with predators and their prey in laboratories or aviaries to large manipulative experiments spanning the latitude. I conduct my research mainly through experimental manipulations, while parts of the research are always also based on the surveys of predator communities, their physiology and patterns in herbivory and defence. This complementary approach of manipulative and observational methods allows me to explore fundamental features of the intricate interactions between plants, their herbivores and herbivore predators. Different approaches also make it possible to understand the problems from different angles and at different levels.

With regard to (i) communication between predators, prey and primary producers, my team focused on this topic mainly in aviaries during experiments when birds were exposed to different stimuli from herbivores feeding on plants. The signals were either visual or chemical, and we were questioning how the predators react to them. Lately, we are trying similar experiments also with various predators (e.g., spiders) and the traces they leave at plants, while investigating how arthropods recognize them and react to them. This work is currently funded and mostly unpublished. As the predators are causing not only direct death to the prey, but they affect also their behaviour, we investigated in several experiments (ii) the indirect effect of predators on insect prey and how could be the fear in insect detected, and how it affects the feeding behaviour. During our research of (iii) gut microbiome, we focused either on simple surveys of gut microbiome in with birds, or we attempted to match the diet with the gut microbiome. In last years, we also conduct various manipulative experiments, where we investigate how is the gut microbiome of hatchlings established during early development, or how the change in diet affects the microbiome (Bodawatta et al. 2018, Bodawatta et al. 2020a, Bodawatta et al. 2020b, Bodawatta et al. 2021a, Bodawatta et al. 2021b, Diez-Méndez et al. 2023).

In addition to me research, I created a new course *Science communication*, which I teach by myself every winter term, and which is voluntary to all PhD and Master students. During the course, I teach and practically test the abilities to communicate their research questions and results/ We communicate with media and practice the outreach of the students' work. I also prepare them for conference contributions and teach them how to prepare talks or posters correctly. During the lectures we not only discuss the scientific sound of the research but also design and graphical tools.

I further developed and teach alone a course of *Field ornithological methods*, which is again voluntary to all Bachelor and Master students. In this course, I teach basic methods of the surveys of birds – first theoretically during several lectures and then practically in the field. We focus on point-counts, line-transect, range mapping, or mist-netting as basic methods during which the students are also taught the bird identification.

I contribute significantly to teaching (e.g., I lead every lecture together with one more lecturer) of *Advances in ecology* and *Practical writing and communication*, where we teach the students to write grant proposals and critically think and discuss scientific papers respectively. Besides these courses to which I contribute significantly, I also teach in several basic courses compulsory for all Bachelor students. Specifically, I teach trophic interactions in *Ecology and environmental protection*, and I lead a lecture and a seminar within course *How to do science*.

I am also often invited to give various university lectures and seminars around the Czech Republic and nearby countries, to participate in summer school programs for PhD students and present simplified presentations for high school teachers and their students. I very often talk to media and assist to PR department with preparation of Open days, Science weeks for grammar school students or even Weekends for grammar school teachers, or Science nights as I really enjoy spreading my passion for my research, and spread the scientific literacy to general public.

Abstract

Tri-trophic interactions (sensu interactions among plants, arthropod herbivores, and their invertivorous predators) play a pivotal role in maintaining ecosystem structure and function, yet their dynamics, especially in terrestrial ecosystems, remain incompletely understood. This habilitation thesis focuses mainly on top-down forces exerted by predators, by exploring the effect of predators on arthropods and on herbivory rates, plant defences and the role they play in interactions between plants and predators, and overall ecosystem processes across spatial gradients.

The research synthesizes extensive field studies, manipulative experiments, and innovative methodologies, including predator-exclosure setups, dummy prey experiments, and dietary analyses as well as analyses of non-lethal effects of predators on prey. Conducted across diverse ecosystems, from tropical forests in Papua New Guinea to temperate forests in Europe or Japan, the thesis evaluates how biotic and abiotic factors modulate top-down control. Key findings highlight that predator-mediated regulation of arthropods significantly reduces herbivory, with stronger effects observed in tropical and low-elevation forests compared to temperate and higher elevations. Additionally, the functional roles of specific predator groups, such as birds, bats, and ants vary with habitat complexity, elevational gradients, and forest strata.

A central theme of the thesis is the interplay between predator-prey dynamics and indirect plant defence mechanisms. The results demonstrate that predator-induced changes in prey density and prey behaviour can influence herbivory patterns and plant fitness, underscoring the importance of both lethal and non-lethal predator effects. In several studies, I showed that birds and bats were effective in mitigating herbivory through direct predation and potentially also by triggering behavioural shifts in prey. Furthermore, my experiments with herbivore-induced plant volatiles revealed that olfactory cues play a crucial role in attracting insectivorous predators to plants, linking chemical plant defences to top-down regulation.

This habilitation thesis also explores the spatial variation of these interactions, mostly along elevational, but also latitudinal or vertical forest gradients. Elevational studies show that predator abundance and effectiveness decline at higher altitudes, while several latitudinal studies do not support the hypothesis that the predator effects are stronger in tropical regions. There, we argue that methodological approaches and ways how predation pressure or predation rate is measured, might have significant effects on the results. The patterns I observed also reflect the influence of climatic, ecological, and evolutionary factors on trophic interactions.

Finally, the introduction of the thesis provides a methodological framework for assessing predator-prey dynamics, incorporating direct observations, camera traps, and molecular tools to overcome the challenges of studying predation in cryptic and complex systems. All of these methods were used in my studies presented in my thesis, but some of them more frequently. These approaches,

and especially their combinations, enable a deeper understanding of the ecological roles of predators and their cascading impacts on lower trophic levels.

In conclusion, this research advances our understanding of the dynamics of trophic interactions, emphasizing the critical role of predators in shaping terrestrial ecosystems. By elucidating the ecological consequences of predator-prey interactions across spatial and temporal scales, my findings contribute to broader ecological theory and might have practical implications for ecosystem management, particularly in the face of global environmental changes that threaten the stability of trophic interactions.

1. Introduction

1.1. On importance of predation (of arthropods)

Empirical evidence shows that predators can be important drivers of elemental cycling within ecosystems by propagating indirect effects that determine the distribution of elements among trophic levels as well as determine the chemical content of organic matter that becomes decomposed by microbes (Leroux and Schmitz 2015). While some predators like wolves or lions are well known, predators can be found in a broad range of taxa, and they feed on various other species. Terrestrial arthropods are a major component of many food webs and common prey or many predators (Rosenberg et al. 2023). Despite that, the impact of predation on arthropods is sometimes neglected. Yet, insectivorous predator-arthropod prey relationships are very important interactions for community ecology, contributing to the ecosystem structure and stability (Rosenberg et al. 2023), as well as adaptive evolution similarly as the interactions between larger predators and their prey (Hairston et al. 1960, Paine 1966, 1980, Pettorelli et al. 2015), and ultimately leading to changes in plant communities (Leroux and Schmitz 2015).

In general, predation of arthropods (as well as other taxa) involves the recognition, capture, handling and consumption of prey by predators, while prey recognize, escape and resist attack (Ishikawa et al. 2018). As arthropod prey is small and abundant, and typically rather harmless against many large invertivorous predators, the interactions between them have many specifics, involving direct and indirect communication. Arthropod prey is also subjected to lethal and/or nonlethal effects from predators. Lethal effects involve predators killing and consuming whole prey, which may then be unable to consume other individuals from lower trophic level, such as plants. With respect to plants, predators may consume chewing herbivores, miners and other groups of herbivores, resulting into decreased herbivory damage (also below the ground). Furthermore, predators can consume pollinators, frugivores, and pollen eaters, thus affecting plant reproduction success (Vanbergen et al. 2018). Predators may further also impact fungivores, bacterivores and impact fungi and bacteria communities, which further affect nutrient cycling (Thakur and Geisen 2019). However, predators can also consume other predators and counterbalance thus the effect of predation on lower trophic levels (Polis et al. 1989, Maguire et al. 2015). With respect to non-lethal effects, for instance, the presence of predators can alter prey behaviour, distribution, habitat choice, foraging and growth (e.g., (Paine 1980, Lima and Dill 1990, Caro 2005, Cooper and Blumstein 2015).

Predation is always influenced by the biotic and abiotic factors. Biotic factors include prey size, (Stearns 1998), predator size, their trophic level interactions (Sih et al. 1985, Oricchio et al. 2016) and habitat complexity (Crowder and Cooper 1982, Mandelik et al. 2003, Mandelik et al. 2012). For example, larger prey experiences higher predation risk (Rodgers et al. 2015) while larger predators increase the predation pressure (Cooper Jr and Stankowich 2010). The risk of predation can vary between and within populations and sites based due to changes in biotic and abiotic factors. First of all,

these factors affect the relative proportions of prey and predators, which are the main drivers of the predation pressure. However, abiotic factors include also environmental temperature directly, background contrast (Herberstein and Fleisch 2003) and light intensity (Brown and Braithwaite 2005, Gaston et al. 2013). For example, when environmental temperature increases, predation can increase since high temperatures increase the energy consumption rate and starvation of predators (Pink and Abrahams 2016).

1.2. Definitions

As we begin discussing predation, it is essential to define terms that are often used interchangeably. The population biology of predation consists of two basic elements: the kill rate and the predation rate (Holling 1959, Taylor and Taylor 1984). **Kill rate** is the number of prey killed per predator per unit time, representing the predator's food supply (Vucetich et al. 2011). **Predation rate**, on the other hand, is the proportion of the prey population killed by predators (Vucetich et al. 2011). Interestingly, this term is sometimes defined without time constraints (e.g., (Vucetich et al. 2011)) and other times with them (Hill and Dunbar 1998). Here, I define and will use the term in the following sense: Predation rate represents the number of prey individuals killed by predation per unit of time. **Predation risk** is defined as the probability of prey death by predation (Hebblewhite et al. 2005, Mumma et al. 2017), or alternatively as the prey's perception of the likelihood of a predator attack, whether or not the attack succeeds (Hill and Dunbar 1998). In this thesis, I follow the former definition. **Predation pressure** acts as a selective force and depends on predator frequency and prey vulnerability. Simply, it can be defined as a function of predation rate and the density of prey and predators, expressing the risk of predation for a specific prey individual based on predator abundance, predation rate, and the presence of other prey. More comprehensively, predation pressure includes aspects like predator detection and attack rates, predator encounter frequencies, and predation efficiency. In this thesis, the term predation pressure represents the risk of predation for a specific prey individual, considering the abundance of predators, their predation rate, and other prey individuals in the surrounding.

2. Approaches to measure predation

Predation in general is difficult to observe, as it is typically swift and elusive moment. Predation of arthropods is even more difficult to observe, as the prey is tiny, swallowed quickly and digested nearly completely. Estimating predation pressure or predation rate requires comprehensive field or laboratory approaches, and not all of the available techniques are suitable for all measures of the predations.

2.1. Direct field observations

This method involves in situ observations of predators and their prey by observers in the field (Sunderland 1988), with the observer either moving or staying at an observation point. This method has been used in predation studies for a very long time. There is however a big difference in the difficulty to observe passive vs. active predators. For example, prey can be easily observed for webbing spiders (passive predators), ants returning to nests with prey (active social predators), or slow predatory larvae (e.g., coccinellids), and with more difficulties in active predators like birds, bats or lizards feeding on arthropods. The method of direct observation allows detection of predation events, predator behaviour and predator/prey abundance, diversity and density, which can be used to measure predation pressure (Sunderland 1988, Jarvis 2007, Vucetich et al. 2011) in natural habitats under natural conditions. Field observations are more reliable and logistically feasible when the prey is exposed, active during daytime, and moves slowly, when predator and prey can be easily identified and when direct observations do not pose disturbances (Pointing 1966). Human error in correct identification of the prey is likely when dense vegetation leads to underestimation of the predation. Alternatively, presence of observer can affect the behaviour of the predators or prey. The observations allow to record predation rate and predation efficiency, and predation successes and failures. In this thesis, I only used direct observations to describe the communities of predators, despite I took the notes on the diet taken, and used such data to define the feeding specialisation of various species (Tvardikova 2013, Sam et al. 2017b, Sam et al. 2024a).

2.2. Camera trap recording

Camera traps have been widely used to monitor predators as soon as the equipment has become more accessible after 1990's. Camera traps capture still images or video footage of predator activity. Because insects are often too small to activate motion sensors, continuous recording is commonly employed to capture arthropod feeding behaviour (Walter et al. 2021). Cameras have successfully documented insect prey being carried to bird nests, as well as to wasp or ant colonies, or other sites with high predator density. However, setting up cameras and equipment in the field can be logistically challenging, often requiring permits and carrying the risk of equipment loss. Environmental factors and technical issues can lead to false triggers and camera malfunctions, resulting in data loss (Birkhofer et al. 2017, Caravaggi et al. 2017, Seimandi-Corda et al. 2024), though more durable, weather-resistant models have been developed (Meek et al. 2020). For certain species, camera presence (due to light and sound) may be intrusive and alter natural behaviour (Meek et al. 2016a, Meek et al. 2016b). In my own work, I currently use the method of camera-trapping as a part of project in which we focus on how the food brought to the nest by bird parents affects the gut microbiome of the chicks (i.e. the topic which is not central to this thesis). We specifically observe which chick on the nest is being fed by what by which parent. Despite the results are promising, the process of prey identification is very demanding. Further

on, I currently use the method of continuous recording in our meadow experiment, where we record pollinators coming to flowers and their interactions with spiders waiting on the flowers.

2.3. Nonmolecular techniques to identify prey from remains of prey

Identification from prey remains involves an examination of predator faecal, gut content or regurgitates for identifying features such as arthropod scales, hairs, mandibles (Hengeveld 1981, Sunderland 1988, Martins et al. 2015). Predators that hunt with traps, such as spiders, often wrap prey into small bundles, which can be removed from the web (Nyffeler 1999) or collected from the burrows that spiders inhabit. This method is advantageous as it involves little or no disturbance to the actual predator-prey interactions. If prey remains can be counted (Symondson 2002, Sam et al. 2017a), then it allows quantification. If the timeframe during which the remains accumulated is known, predation rate could be estimated. However, in many of these methods, ethical concerns arise, as the predators need to be handled, more or less invasively. Non-molecular methods depend heavily on coarse identifications, which can be time consuming and not precise, especially in prey rich sites. Data can be skewed, as soft-bodied prey can be fully digested and not traceable from the regurgitates or gut remains. It is important to note, that identification of the prey remains is unlikely to provide spatial and temporal resolution, and it only represents successful consumption events. Gut analyses are further affected by different rates of digestion of the prey items. Thus, this method is useful for quantification of the predator diet and possibly predation rate. During my own work, I analysed diet from remains of prey several times for various purposes (Sam et al. 2017a, Camille et al. 2020, Bodawatta et al. 2022).

2.4. Molecular identification of prey items

Molecular techniques enable the detection of prey-specific proteins or DNA in the gut, regurgitate, or faecal samples of predators, which is especially crucial for identifying prey that may be entirely digested. The enzyme-linked immunosorbent assay (ELISA) has become widely used in predator gut content analysis, as it can detect proteins unique to specific prey species as well as proteins indicative of particular life stages (Harwood et al. 2007). Other powerful methods, including polymerase chain reaction (PCR), DNA sequencing, and DNA barcoding/metabarcoding, have emerged as key tools for dietary analysis in predators (Traugott et al. 2013, Wang et al. 2022). For instance, next-generation sequencing has been successfully applied to identify prey species in the gut and faecal contents of diverse predators like spiders, skinks, and birds, helping to clarify if ant-mimicking species are targeted by these predators (Pekar et al. 2017). Real-time quantitative PCR (qPCR) has more recently allowed for the precise quantification of springtail DNA within spider gut samples (Symondson 2012, Sun et al. 2021). However, these molecular approaches often require prior knowledge of the prey taxa (Greenstone et al. 2014, Furlong 2015) and may not differentiate between predation and other types of prey acquisition, such as scavenging, secondary predation, or cannibalism (Greenstone et al. 2014,

Furlong 2015). Furthermore, they depend on sophisticated laboratory equipment and highly controlled conditions (Murray et al. 2011). Most importantly, contamination and DNA degradation in the predator gut may result in misidentifications, and degradation of plant material can cause inhibition of the reactions, preventing the isolation of animal DNA (Symondson 2002). In my own work, I relied on the molecular identifications of the prey in several studies (Bodawatta et al. 2020a, Bodawatta et al. 2021b).

2.5. Predation on a dummy prey

Prey identification from predation marks on dummy prey is a widely used experimental technique in ecological research to investigate predator-prey dynamics and assess predation pressure in various habitats. Dummy prey, often crafted from pliable materials such as plasticine or clay, are deployed in the field to mimic natural prey while providing a durable and easily analysable surface (Howe et al. 2009). When predators attack these models, they leave physical imprints—such as beak impressions, tooth punctures, or claw scratches—that are species- or guild-specific, allowing researchers to infer predator identity (Low et al. 2014). For instance, birds often leave sharp, V-shaped punctures or linear scratches, whereas mammals may leave rounded punctures from teeth or gnaw marks. Additionally, insect predators like ants can leave distinctive mandibular patterns or fine abrasions. This method is particularly advantageous for studying cryptic or nocturnal predators that are difficult to observe directly, or for relative comparisons of the predation rates (Howe et al. 2009).

The approach is especially valuable in ecological studies of forest systems, where direct observations are challenging. It enables researchers to quantify spatial and temporal variations in predation pressure, assess predator diversity, and evaluate the influence of environmental variables such as habitat structure or prey visibility on predation rates. However, these measures can be taken only as relative – one can compare by this method predation in two habitats, but for example not the importance of various predators, as different predators react to prey differently (Howe et al. 2009). Furthermore, when combined with other survey methods, dummy prey studies can elucidate the functional roles of specific predator groups in ecosystem processes. By providing a standardized and replicable framework for data collection, this method contributes significantly to our understanding of predator-prey interactions across diverse ecosystems and scales, and it aligns well with modern efforts to link ecological patterns with underlying processes.

Typically, the dummy prey are green caterpillars, but reactions of predators to various colours can be tested (e.g. Howe et al. 2009, Howe et al. 2015, Roslin et al. 2017, Valdés-Correcher et al. 2022). Attacks have been recorded also on different models – for example of poisonous frogs (Hegna et al. 2011), dummy surfaced earthworms (Vinogradov et al. 2024), and very typically the plasticine eggs are used in the experiments estimating predation of eggs on the nest (Purger et al. 2012). Sometimes, models are made of paper (Mc Key 2024), or combination of plasticine and paper (e.g., for butterflies where they body is from plasticine and wings from paper). By myself, I used and described the method several

times (e.g., Sam et al. 2015a, Sam et al. 2015b, Sam et al. 2022b), and our attack identification collection is widely used (Low et al. 2014).

2.6. Predator enclosure/exclosure experiments

Modern enclosure experiments are instrumental in disentangling the effects of top-down control by predators on prey populations, community composition, and ecosystem functions (Schmitz 2004, Bakker et al. 2016). Exclosure studies have demonstrated that predator removal can lead to increased herbivore abundance, resulting in altered vegetation structure and ecosystem processes (Beard et al. 2003, Bakker et al. 2016). However, the effects of predators on ecosystems can be context-dependent and influenced by factors such as omnivory (Johnson et al. 2014). These experiments provide valuable insights into the complex interactions within food webs and the cascading effects of predator loss on ecosystem functioning. For example, in tropical forest systems, exclosure setups have been used to study the cascading effects of bird and bat predation on herbivorous insects and their impact on tree seedling growth and survival (Van Bael et al. 2003, Van Bael and Brawn 2005, Sam et al. 2023). In grassland ecosystems, the exclusion of mammalian predators like foxes has demonstrated their role in regulating rodent populations, with cascading effects on plant seed dispersal and soil disturbance (Ramasamy et al. 2020). Similarly, aquatic systems have employed exclosures to assess the impact of predatory fish or invertebrates on algal growth and nutrient cycling (Persson 1997, Eriksson et al. 2009).

The first publication focusing on the manipulation of predators to evaluate their effect on lower trophic levels was published in 1976 (Solomon et al. 1976), and since then, many similar studies are being conducted every year. Most of these studies have described the effects of vertebrate (birds and/or bats) and ant exclusion separately. Vertebrates are typically excluded by cages, which are permanently placed around the trees/shrubs etc., while the cages are made of wooden or metal constructions and covered by netting, or of metal meshes (Van Bael et al. 2003). Ants on the other hand, are often excluded by sticky barrier like tangle foot or other agricultural sticky barriers (Boiteau and Vernon 2001, Qureshi and Stansly 2009). Few exclusion experiments have considered both vertebrates and ants, and even fewer have aimed to exclude lizards (Dial and Roughgarden 1995, Borkhataria et al. 2006). Recently, factorial experiments treating insectivorous birds and bats as separate variables have started to appear and shed light on their relative effects on arthropods. I summarized this topic in one meta-analysis and one book chapter (Sam et al. 2022c, Sam et al. 2024b), while I use the factorial design often during the field experiments (Houska Tahadlova et al. 2022, Sam et al. 2023, Sivault et al. 2024a, Sivault et al. 2024b)

3. Tritrophic interactions

3.1. Top-down control

Top-down control describes the regulatory influence of higher trophic levels on lower ones, primarily through predation and its cascading effects on herbivores and primary producers. This mechanism is fundamental to the trophic cascade hypothesis, which posits that predators indirectly enhance primary production by limiting herbivore populations. Such processes are particularly significant in forest ecosystems, where structurally complex habitats foster intricate food webs and interactions.

Top-down trophic control is generally stronger in aquatic ecosystems than in terrestrial ones (Shurin et al. 2002), and examples of trophic cascades involving terrestrial mammals remain relatively rare (Schmitz et al. 2000). However, mammalian apex predators are considered crucial regulators of trophic structure and biodiversity in terrestrial ecosystems (McLaren and Peterson 1994, Palomares et al. 1998, Terborgh et al. 1999, Terborgh et al. 2001) (Sinclair et al. 2003). These predators not only affect herbivore populations but also prey upon smaller predators in lower trophic levels (Palomares and Caro 1999). Consequently, declines in top predator populations can lead to mesopredator release, whereby an increase in medium-sized predator abundance negatively impacts prey communities (Crooks and Soulé 1999). Mesopredator release occurs in terrestrial and marine ecosystems; and for instance, in North America, the ranges of all apex carnivores have contracted whereas those of 60% of mesopredators have grown in the past two centuries (Prugh et al. 2009).

In many forest ecosystems, insects consume a substantial portion of woody plant biomass, and their populations are regulated by insectivorous predators. These predators, including birds, mammals, lizards, and ants or spiders, play a pivotal role in controlling herbivore populations, thereby reducing herbivory and promoting plant growth. The structurally complex environments of forests amplify these interactions, with predator-prey dynamics varying across spatial scales, forest types, and climatic conditions. Habitat structural complexity is considered an important factor influencing the population dynamics and trophic organization of terrestrial arthropod (Price 1980, Langellotto and Denno 2004). By incorporating the effects of habitat structure on higher trophic levels, it is possible to more thoroughly understand the extent to which top-down effects from natural enemies cascade throughout a food web (McCoy and Bell 1991, Denno et al. 2002).

Predator effects extend beyond direct predation. They also trigger behavioural changes in herbivores, such as avoidance or reduced feeding activity, amplifying their impact on forest dynamics (Lima 1998). While each predation event only influences a single prey per unit of time, the risk introduced by the mere presence of a predator could have more widespread effects by causing many prey individuals to significantly alter their foraging behavior (Cinel et al. 2020). Moreover, trade-offs are probably included in insect prey responding to various threats. For example, the presence of invertebrate predators can reduce the resistance of insects to pesticides (Op de Beeck et al. 2016) and the nonlethal effects of predators can thus further affect prey mortality and impact ecosystem

functioning. Understanding such nonlethal effects of insectivorous predators is especially important as insects are the most dominant animal group on Earth (Stork et al. 2015), and non-lethal effects on them can have tremendous impacts on the consumption of the plant biomass (Werner and Peacor 2003, 2006, Kollross et al. 2022).

3.1.1. Top-down control along elevations

Elevational gradients provide valuable natural laboratories for studying how abiotic factors and spatial variability shape ecological processes like trophic cascades. Unlike latitudinal gradients, which may be confounded by factors such as dispersal limitation (Salisbury et al. 2012), elevational studies allow for the examination of intra- and interspecific patterns at comparable scales and within similar climatic zones (e.g., Colwell et al. 2016, Beck et al. 2017). These studies can also be replicated within and across regions (e.g., Sanders 2002, Grytnes et al. 2014).

As elevation increases, abiotic conditions shift, including reduced nutrient availability (Salinas et al. 2011, Fisher et al. 2013), declining temperatures (Barry 1992), and generally higher precipitation and solar radiation (McCain 2010). These changes indirectly affect biotic interactions by altering the composition, abundance, and dynamics of predator, plant, and herbivore communities (McCain 2010). Consequently, the strength of top-down forces is expected to vary along elevational gradients (Sam et al. 2015a, Roslin et al. 2017).

For example, studies on bats and birds indicate that species richness often decreases with elevation in tropical regions or follows a unimodal trend in temperate areas (McCain 2005, 2007, McCain 2009, McCain 2010). Peaks in bat species richness occur where water availability and temperature are both high, typically at low or mid-elevations in tropical mountains and temperate ranges, respectively (McCain 2007). Variations in species richness and functional diversity may significantly influence the role of insectivorous bats in top-down processes along elevational gradients.

However, predator exclusion experiments are often limited to single locations (Philpott et al. 2004, Kalka et al. 2008, Williams-Guillén et al. 2008, Beilke and O'Keefe 2023) and sometimes to a single season (Kalka et al. 2008, Maas et al. 2013, Cassano et al. 2016, Gras et al. 2016, Ferreira et al. 2023). This restricts our understanding of how trophic interactions respond to climatic and environmental variability. This is why I and my team investigated how elevational changes impact predator-mediated top-down interactions across multiple elevations (Sam et al. 2023, Sivault et al. 2024a)

3.1.2. Top-down control across forest strata

The complexity of food webs leads to variability in the strength of top-down control, both among forests and within different vertical strata of the same forest (Van Bael et al. 2003, Bohm et al. 2011). Forests comprise multiple layers, each characterized by unique vegetation, light availability, and ecological

niches. Canopy and understory layers often represent two extremes of the vertical gradient, and only few studies focused on vertical strata in the mid heights. The canopy, located at the top, is more exposed to thermal and hydric fluctuations than the understory (De Frenne et al. 2021). It generally experiences higher temperatures, increased sunlight and wind exposure, and lower humidity (Parker 1995). Other factors distinguishing the canopy include tree height, spatial arrangement, biomass, and the size and abundance of leaves, flowers, and seeds (Lawton 1983). These differences foster distinct ecological niches, influencing the availability and quality of arthropod food resources (Basset 2001, Basset et al. 2001), which in turn shape the distribution of prey and their predators.

Substantial evidence documents the vertical stratification of arthropods and their predators in forests (McCaig et al. 2020, Basham et al. 2023). For instance, a recent review by Basham et al. (2023) highlighted that bats in tropical forests generally exhibit higher richness and abundance in the canopy, and similar patterns were found for birds (Chmel et al. 2016). In temperate forests, however, stratification patterns are inconsistent, with no clear layer preference within guilds (Froidevaux et al. 2014) or species-specific differences in activity between strata (Plank et al. 2012, Moreno-García et al. 2014). These differences are often linked to factors such as foraging behaviour (Bernard 2001), and predator avoidance (Rex et al. 2011), as well as competition for resources (Rader and Krockenberger 2006, Chmel et al. 2016). Despite these findings, limited canopy access has historically constrained comprehensive ecological studies. Questions regarding the role of stratification in trophic cascades and comparisons of top-down forces across strata remain underexplored (Van Bael et al. 2003, Bohm et al. 2011, Sivault et al. 2024b).

3.1.3. Top-down control across latitude

Latitudinal gradients, like elevational ones, provide a natural framework for studying ecological processes. However, latitude encompasses a broader range of variables, including historical, geographical, biotic, abiotic, physical, and stochastic factors (Mittelbach et al. 2007, Mittelbach and Schemske 2015). Primary environmental gradients, such as temperature, solar radiation, and seasonality, are often interrelated, complicating hypothesis testing and leading to controversial findings. This complexity remains a significant challenge in developing comprehensive ecological theories.

Nonetheless, previous studies suggest that top-down forces on herbivores are stronger in tropical regions (Rodríguez-Castañeda 2013, Roslin et al. 2017, Zvereva et al. 2020), supporting the hypothesis that biotic interactions are more pronounced at lower latitudes (Pennings and Silliman 2005, Schemske et al. 2009). The greater diversity and density of predators like birds and bats in tropical forests compared to temperate ones (Maas et al. 2016) reinforce this idea. However, debates persist about whether top-down forces vary consistently along latitudinal gradients, with some studies finding no differences in productivity levels (Borer et al. 2006, Mooney et al. 2010). Given the complexity of food webs and local environmental influences, top-down forces likely vary between sites (Gripengberg

and Roslin 2007). As with elevational gradients, latitudinal changes and their associated abiotic and biotic factors are expected to influence the strength of predator-mediated top-down interactions.

In my own work, I focused with my students or colleagues on the latitudinal patterns in several studies. First, we found there is higher predation rate on dummy prey in the tropics than in temperate forest (Roslin et al. 2017), then we observed different predation rate patterns on the dummy vs. live prey (Zvereva et al. 2024), and then we did not find support for higher predation via predator enclosure experiment (Chapter 5, (Sivault 2024))

3.2. Bottom-up control and plant defences

Bottom-up control refers to the ecological concept where ecosystems are primarily regulated by the availability of nutrients, light, or water, which influence primary production and subsequently impact other ecosystem functions. While top-down control shapes ecological interactions through predator-prey dynamics, bottom-up forces set the foundation for these interactions (Power 1992, Denno et al. 2002, Gruner 2004). This suggests that bottom-up forces determine the maximum productivity and range of possibilities in an ecosystem, while top-down forces govern details of realized growth and structure (Gutierrez et al. 1994). In this thesis, I investigate the bottom-up forces rather indirectly, via the productivity of different environments along gradients and via plant defences. Plant defences, as part of the bottom-up forces, act as mechanisms by which plants control herbivore pressure and modulate the efficiency of energy transfer to higher trophic levels.

Plants deploy a wide range of defensive strategies to mitigate herbivory, which can be broadly categorized as direct and indirect defences (Hanley et al. 2007, War et al. 2012, Kant et al. 2015). Both types of defences are profoundly influenced by environmental factors, including those that vary along various gradients – elevational, vertical, latitudinal, and in general with any change in productivity and nutrient availability.

3.2.1. Direct plant defences: Physical and chemical barriers

Direct plant defences involve structural and chemical traits that reduce herbivory by deterring or incapacitating herbivores. Physical barriers such as thick cuticles, spines, trichomes, or lignified tissues impede herbivore feeding and access (Hanley et al. 2007). Physical defences are effective in deterring larger herbivores and those with chewing mouthparts (e.g., chewing arthropods). These barriers can reduce herbivore access and feeding, but they are advantageous also in environments with high mechanical stress, such as windy or arid conditions. Sometimes it is difficult to exactly determine, against which factors are the physical defences aimed originally. However, physical barriers might be less effective against smaller or specialized herbivores like leaf miners or sapsuckers. These traits are often more pronounced at higher elevations (Körner 2007). Conversely, some studies indicate that increased ultraviolet radiation and lower temperatures at higher elevations drive the accumulation of

secondary metabolites, enhancing chemical defences like alkaloids, tannins, and phenolics (Pellissier et al. 2012, Pellissier et al. 2014, Rasmann et al. 2014, Salgado et al. 2016). Chemical defences, such as alkaloids, tannins, and phenolics, target a broader range of herbivores by interfering with their digestion, metabolism, or development (War et al. 2012). These barriers are particularly effective in environments with high herbivore diversity and pressure. Additionally, chemical defences can be more adaptive, with plants increasing their production in response to herbivore damage.

The development of chemical defences in plants is closely tied to the production of secondary metabolites - organic compounds that are not directly involved in essential processes like photosynthesis or basic metabolism. These compounds, which include phenolics, flavonoids, and tannins, are often synthesized as by-products of primary metabolic pathways (Fraenkel 1959, Whittaker 1970, War et al. 2012). Traditionally, secondary metabolites have been regarded as crucial for protecting plants against herbivores (Fraenkel 1959, Whittaker 1970). However, a meta-analysis of recent studies suggests their role in plant defence might be less significant than previously thought or potentially more intricate when compared to primary chemical and physiological traits (Carmona et al. 2011).

3.2.2. Indirect plant defences: attracting natural enemies

Plants often protect themselves by enlisting the help of natural enemies to suppress herbivores, a strategy known as indirect defence (Dudareva et al. 2006). These defences can be either constitutive (i.e., always present) or activated in response to specific attacks, involving a combination of physical damage and chemical signals from herbivores. For instance, plants produce volatile organic compounds (VOCs) which attract predators and parasitoids to reduce herbivore populations (Dudareva et al. 2006, Maffei 2010). Plants typically release low levels of volatiles even under normal conditions, but herbivory triggers a distinct blend unique to the plant-insect interaction - herbivore-induced plant volatiles (HIPVs, i.e., VOCs induced by herbivore activity). Sometimes, the HIPV blend not only attracts natural enemies but also signals to neighbouring plants and undamaged parts of the same plant, priming their defences (Arimura et al. 2009).

These volatiles are blends of various compounds that can deter herbivores or attract their natural enemies (Dudareva et al. 2006). HIPVs are lipophilic and they can be released from the leaves, flowers, fruits, and even roots when plants are attacked (Dudareva et al. 2006). The specific HIPVs produced depend on the plant and herbivore species and their feeding style, their developmental stages – as these activate different signalling pathways, resulting in the production of specific volatile compounds (Walling 2000), and environmental factors (Arimura et al. 2009, Maffei 2010). Furthermore, HIPV production can be experimentally induced by the external application of plant hormones, which play a crucial role in the biosynthetic pathways responsible for their formation.

HIPVs include terpenes, green leafy volatiles (GLVs), ethylene, methyl salicylate, methyl jasmonate, monoterpenes (e.g., myrcene, β -ocimene), sesquiterpenes (e.g., α -farnesene), homoterpenes and other VOCs (Dudareva et al. 2006). These volatiles either repel or deter herbivores directly or attract

predators and parasitoids to protect plants. (Dudareva et al. 2006, Matsui 2006) For example, methyl salicylate have been shown to attract predatory mites (De Boer et al. 2004). Methyl jasmonate was reported to attract parasitoids (Thaler et al. 1996, Thaler 1999, Thaler et al. 2012, Heil 2014), and even birds (Mäntylä et al. 2014, Mrazova and Sam 2019). Similar compounds, such as methyl benzoate, also play a role in attracting natural enemies (Xiao et al. 2024). However, this strategy carries ecological risks, as HIPVs can sometimes attract pests (Dickens 2006).

The emission of HIPVs occurs within hours of herbivore infestation (Dudareva et al. 2006, Holopainen and Blande 2013). The timing and composition of volatile release vary by plant species (Dudareva et al. 2006, Holopainen and Gershenzon 2010), and the mutualistic relationships between plants and their natural enemies are thus very variable (Heil 2008, Heil and Karban 2010, Heil 2014)

Some plants have evolved mutualistic relationships with ants by providing specialized structures or resources, such as hollow stems, swollen thorns, or food bodies and/or secrete extra floral nectar (EFN), to house and sustain ant colonies (Koptur 2005). In return, the ants protect the plants from herbivores and even competing vegetation. This mutualism can be highly effective; ants actively patrol the plant's surface, attacking herbivorous insects and deterring other potential threats. Additionally, some ant species clear surrounding vegetation, reducing competition for light and nutrients. Many of the ant enclosure experiments (discussed above) thus provide equivocal results, depending on the specific roles of ants in the given system. In general, indirect plant defences has garnered significant attention, with studies investigating its genetic, biochemical, physiological, and ecological aspects (Dudareva et al. 2006, Maffei 2010).

3.2.3. Vertical stratification of bottom-up defences

Bottom-up defences in plants are also stratified vertically within forest layers. In the canopy, where light intensity and UV exposure are high, plants often exhibit thicker leaves with greater concentrations of phenolics and flavonoids to combat oxidative stress and deter herbivores (Rozendaal et al. 2006, Escobar-Bravo et al. 2017). These compounds provide photoprotective properties while serving as chemical deterrents to generalist and specialist herbivores. Additionally, canopy leaves may exhibit increased trichome density, which further reduces herbivory by impeding insect movement and feeding (Molina-Montenegro et al. 2006, War et al. 2012).

Conversely, in the shaded understory, plants tend to prioritize mechanical defences such as increased leaf toughness or higher fiber content to deter chewing herbivores (Coley and Barone 1996, Kitajima and Poorter 2010). Thick cell walls and higher lignin content in understory leaves not only deter herbivores but also enhance leaf longevity, which is crucial in low-light environments where energy for leaf production is limited (Poorter et al. 2009). These mechanical defences are particularly effective against larger herbivores, such as caterpillars, that dominate understory herbivore assemblages.

These differences in defence allocation reflect the distinct environmental pressures and herbivore communities associated with each stratum (Basset 2001, Richards et al. 2015). Herbivore diversity and abundance are typically higher in the canopy, where a greater variety of insect species exploit available niches (Basset 2003). Moreover, VOC emission patterns may differ between canopy and understory layers, with canopy plants emitting more volatile compounds due to greater air circulation and herbivore diversity (Peñuelas and Llusà 2004, Holopainen and Gershenson 2010). These volatiles not only serve to deter herbivores directly but also play a crucial role in indirect defences by attracting predators and parasitoids of herbivores (Dicke and Baldwin 2010).

3.2.4. Elevational impacts on bottom-up defences

Changes in nutrient availability, temperature, and light along elevational gradients affect both direct and indirect defences. Nutrient-poor soils at higher elevations may limit the production of nitrogen-based chemical defences, favoring carbon-based compounds like lignin and tannins (Bryant et al., 1983). In contrast, low-elevation forests with abundant herbivore pressure may drive plants to invest more heavily in diverse chemical defences and mutualistic relationships with natural enemies (Dyer and Coley 2001). It is generally thought that herbivore pressure is higher at lower elevations where climate is warmer and less seasonal, and that this has led to higher levels of plant defence investment at low elevations (Rodríguez-Castañeda et al. 2010, Pellissier et al. 2012). However, the generality of this expectation has been called into question by recent studies (Rasmann et al. 2014, Abdala-Roberts et al. 2016).

Most research on altitudinal gradients in plant defences and herbivory has implicitly assumed a causative link between amounts of herbivore damage and concomitant plant allocation to defences (Rasmann et al., 2014). However, it is also well recognized that herbivory is influenced by other plant traits not associated with resistance, such as traits associated with nutritional status (Karban 1992, Agrawal 2007). Nutrient concentrations in plant tissues (e.g., nitrogen, phosphorus) are usually low in relation to insect nutritional demands, which frequently makes nutrients a limiting factor for herbivores, and in some cases, they are better predictors of herbivory than defences (Carmona et al. 2011).

3.3. Perception of insect prey and indirect plant defences by predators

The perception of insect prey and indirect plant defences by predators is a critical driver of ecological interactions, shaping food web dynamics, predator-prey relationships, and plant defensive strategies. For sure, the plant indirect defences would be of a little use, if there were no predators which would respond to them. All predators rely on a range of sensory modalities- including visual, olfactory, and auditory cues - to detect, locate, and capture insect prey.

3.3.1. Vision

Many of the predators rely on visual cues, when orienting themselves towards the prey. They can see not only the prey directly, but they can use various cues left by the prey. For example, some birds were

shown to orient themselves towards excrements of caterpillars left on the foliage (Waldbauer 2012). We have also shown that birds prefer to search for prey on the leaves which have visible holes on them, indicating the insect prey being around (Sam et al. 2015a). On the other hand, some caterpillars effectively use rolls and hid themselves inside the foliage, escaping thus to birds (Tvardikova and Novotny 2012). Many species of insectivorous birds have forward-facing eyes, providing binocular vision that enhances depth perception, crucial for accurately targeting fast-moving or camouflaged insects. Vision is especially important during flight, as birds must rapidly process visual information to maneuver through complex environments while pursuing prey (Blackwell 2002, Emery 2006, Waldbauer 2012, Martin 2022, Niu et al. 2022).

In insectivorous bats, vision plays a secondary role to echolocation in prey detection and navigations. Vision helps these bats orient themselves in their environment, especially over longer distances or in low-light conditions where echolocation is less effective (Gorresen et al. 2015, Danilovich and Yovel 2019). Many insectivorous bats have eyes adapted to dim light, allowing them to perceive large objects, detect movement, and avoid obstacles during flight. Vision can also assist in foraging by helping bats identify open foraging areas or recognize landmarks for roosting. In certain scenarios, such as flying in open spaces or under moonlight, vision may complement echolocation by providing additional spatial information (Bell and Fenton 1986, Danilovich and Yovel 2019, Davies et al. 2020). Some species may rely more heavily on vision during twilight or when targeting large, slow-moving prey that does not produce strong echolocation echoes.

Majority of non-flying mammals, lizards and amphibians rely heavily on vision for detecting prey, navigating their environment, and communicating with conspecifics (Morrison 1980, Fleishman 2024). Many have excellent color vision, with lizards having the ability to perceive ultraviolet light (i de Lanuza and Font 2014), which helps them detect insect prey. Their eyes are adapted for spotting movement, allowing them to react quickly to fast-moving prey or predators. Some species, like chameleons, have independently moving eyes, giving them a wide field of view and precise depth perception. Similarly, amphibians like frogs and salamanders use vision to locate prey, with their large, forward-facing eyes providing excellent night vision and motion detection. Many non-flying mammals have a visual range adapted to low-light environments, making them effective hunters of insects and other small prey at dusk or during the night (Morrison 1980).

Insectivorous ants and other predatory insects rely on a combination of vision, chemical cues, and tactile senses to locate and capture prey. While their visual range is typically limited compared to vertebrate predators, many ants can detect movement and differentiate between light and dark at distances of a few centimeters to several meters, depending on the species (Graham and Philippides 2017, Aksoy and Camlitepe 2018). For example, arboreal ants such as *Oecophylla* (weaver ants) have relatively good eyesight, enabling them to spot prey or intruders from several body lengths away (Offenberg 2021, Ogawa et al. 2023). Ground-dwelling species often depend more on chemical trails and vibrations but still use vision to detect nearby prey (Cerdá and Dejean 2011, Dejean et al. 2024).

Spiders, particularly active hunters, rely heavily on vision to detect prey. Actively hunting spiders have some of the most acute vision among arthropods, with their large, forward-facing principal eyes providing sharp, colour, and even UV vision. They can detect prey from a distance of up to 20-30 centimeters. Their secondary eyes offer a wider field of view, helping them track movement and navigate their environment. Some have excellent vision, allowing them to hunt effectively at night by detecting slight movements of prey in low light. However, web-building spiders typically have poorer eyesight and rely more on vibrations transmitted through their webs to sense prey.

3.3.2. Olfaction

Olfaction in insectivorous birds is less prominent than vision but still plays a role in specific contexts, and very important role in some species (Roper 1999). Some species can detect the chemical cues emitted by their prey directly, or the volatile odours from plants caused by insect activity (HIPVs)(Gagliardo 2013). The attractivity of the volatiles compounds for insectivorous birds have been studied several times now, and while some studies failed to support the use of olfactory by birds (Koski et al. 2015, Mrazova et al. 2019), many studies (especially those conducted in natural environment) supported this theory. I investigated the olfactory in birds in several empirical studies and also reviewed the topic twice (Mrazova et al. 2019).

Frugivorous and nectar feeding bats are known to rely on olfactory cues which help them to locate ripe fruits (Rieger and Jakob 1988, Hodgkison et al. 2013). In insectivorous birds, the use of olfactory remain understudied, but there are indications that they use it also, at least in some cases, as a secondary sense. It remains unknown whether bats could use also plant induced volatile compounds for navigations towards prey rich sites (Zhang et al. 2024).

Lizards often use their vomeronasal organ (Jacobson's organ) to detect chemical cues from prey, which they gather by flicking their tongues (Hirschler 2024). Frogs and toads use olfactory cues to detect the specific scent during search for their home ponds of water (Vyatkin and Shakhparonov 2024) or the chemical signatures of prey in water (Gazzola et al. 2024). In both lizards and amphibians, olfaction plays a complementary role to vision, enhancing their ability to hunt effectively. Neither lizards, nor amphibians were shown to use herbivore-induced plant volatiles (HIPVs) in the same way that insectivorous birds or parasitoids might.

Olfaction is a primary sense for ants and many other predatory insects, playing a crucial role in foraging and prey detection (Hölldobler 1978). Ants use their antennae to detect chemical trails, pheromones, and the scent of prey from several centimeters to meters away, depending on the concentration of the odor (Hölldobler 1978, Renyard 2024). Ants are known to react strongly to various plant induced volatile compounds (Yan et al. 2024). Many ant species are known to follow the trails of HIPVs released by plants, which helps them find new foraging sites or detect high-density patches of herbivores (Müller 2024).

In spiders, olfaction is less developed than in insects, but they can still detect airborne chemical cues, especially through specialized sensory hairs called trichobothria (Barth 2000, Uhl 2013). Some actively hunting spiders, use olfactory signals to recognize potential prey or mates (Hostettler and Nentwig 2006), while web-building spiders are expected to rely on the chemical cues a bit less. Olfaction also helps certain species identify prey-rich environments or recognize chemical trails left by other organisms, to avoid own predators or competitors. Some studies suggest that spiders can detect the presence of HIPVs in the air and may adjust their hunting behavior based on the concentration of herbivore-induced emissions (Li et al. 2024, Shannon and Rypstra 2024), but some studies contradict the usage of the HIPVs by spiders (Oyarzabal et al. 2024).

4. Invertivorous predators

Insectivorous predators play crucial roles in shaping ecosystems through top-down control of herbivorous arthropods. Their influence varies significantly across habitats, including mainland and island ecosystems, as well as along elevational gradients and vertical forest strata. This variability reflects differences in species richness, population densities, and ecological roles across spatial and environmental gradients. Below, we examine key groups of insectivorous predators - birds, bats, ants, lizards, and spiders – in the context of the factors mentioned above, i.e. the factors I focused on in my work (**Table 1**). They all differ in their abilities to colonize and inhabit different habitats and elevations, or in their energy needs and diet breadth, thus having different effects on the prey and further on the plant herbivory damage.

4.1. Birds

Insectivorous birds, as highly mobile predators, are nearly ubiquitous and colonizing even islands and very high elevations relatively easily. In tropical forests, insectivorous birds consume 100–176 kg of insects per hectare annually, while in temperate forests, this value ranges from 35 to 137 kg per hectare annually (Nyffeler et al. 2018). Along elevational gradients, a similar decline in diversity and complexity is observed, with fewer species at higher elevations and greater dietary supplementation as arthropods become scarcer (Sam et al. 2017b). With lower availability of land space in mountains, the birds in high tropical mountains keep reportedly relatively higher densities per land area, which might further add a predation pressure on relatively less dense arthropods (Sam and Koane 2020). Bird's species richness is often reduced on islands, and some species exhibit there higher population densities compared to mainland counterparts (Wright 1981, George 1987), very likely for the similar reasons as high mountain birds keep more dense populations at high elevations. On islands, bird diets often broaden to include flowers and nectar due to limited arthropod diversity. This dietary flexibility may imply greater predation pressure on insects compared to the mainland (Nilsson and Ebenman 1981). Along the elevational gradients in general, theoretical models suggest a plateau in predation pressure at

lower elevations, with diminishing impacts at higher elevations and we observed such patterns in many (but not all) of our empirical studies (Tvardikova and Novotny 2012, Houska Tahadlova et al. 2022, Sam et al. 2023). Patterns vary along mountains with different humidity and thus diversity (and productivity) patterns (Sam et al. 2022c).

4.2. Flying mammals - bats

Bats (order: Chiroptera) make up about 22% of all mammal species, with a total of over 1,462 known species worldwide (Simmons and 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. Almost 70 % of the species known are insectivorous (Fenton and Simmons 2020). 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 (Kurta et al. 1989, Kalka and Kalko 2006) 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 (e.g., Heim et al. 2017). Bats constitute also a significant portion of mammalian diversity on oceanic islands, with 60% of bat species inhabiting islands, and 25% of these being island endemics (Jones et al. 2009). However, island bat communities tend to be less diverse and dominated by frugivores with strong dispersal abilities (Meyer and Kalko 2008). Richness and abundance of insectivorous bats decline sharply with elevation (McCain 2004, McCain 2005, Sivault et al. 2023).

The predation by bats is difficult to survey, as they are active in night and in motion mostly. Many methods are not suitable for them. Also, abundances are difficult to obtain. Therefore, the predation by bats is surveyed via exclosure experiments, which often neglected the effect of the bats. Typical exclosures are placed permanently, summarizing thus the effect of birds and bats. Today, there is more and more exemptions in the current literature, and I attempted to separate the effect of bats in birds in several studies (Chapter 5 in Sivault 2024, Sivault et al. 2024b)

4.3. Non-flying mammals

Non-flying mammalian insectivores, which are for example hedgehogs, shrews, echidnas, anteaters, pangolins, numbats, armadillos and others, exhibit notable species richness and play an important ecological role globally. However, only smaller number of them attack insect on the foliage of trees, due to their body size (Lovegrove 2000). On the trees, insect is typically eaten by shrews. There are over 450 species of shrews alone, making them one of the most species-rich groups among small mammals (Churchfield 1990). These insectivores are widespread, inhabiting a range of environments, from temperate forests and grasslands to tropical rainforests.

Globally, their biomass can be substantial, particularly in regions where high densities of small insectivorous mammals contribute significantly to energy flow and ecosystem functioning. For example, in temperate forest ecosystems, the biomass of shrews can rival that of larger herbivores, reflecting their high metabolic rates and continuous need for insect prey (Churchfield 1990, Lovegrove 2000). In tropical systems, insectivorous mammals are less dominant in biomass compared to birds or bats but still contribute to maintaining insect population balance, particularly in the soil and litter layers. To my knowledge, there is no study trying to manipulate the presence of insectivorous mammals, and we recorded the mammal attacks on dummy prey only very rarely (Low et al. 2014, Sam et al. 2015a, Roslin et al. 2017, Mrazova and Sam 2019).

4.4. Amphibians and reptiles

While a comprehensive global count is challenging, it is clear that a diverse range of reptilian species, particularly lizards such as geckos or chameleons, play a significant role in arthropod consumption. Some small snake species also rely on arthropods as a food source (Parga Jr, 2018). Amphibians (frogs, toads, salamanders) are also significant invertivorous predators, consuming large amounts of arthropods, even those toxic one, as they do not seem to be affected by alkaloids present (Sloggett, 2012).

Lizards, with their low energetic requirements, can achieve high densities following predator or competitor release, particularly on islands (Pough 1973, Schoener and Spiller 2010) or other less suitable habitats. There has been several manipulative studies changing the densities of lizards on islands (Spiller and Schoener 1990, Schoener and Spiller 2010). Unlike from amphibians, diet of lizards often diversify to include plants, which allows them to thrive in resource-limited island environments (Buckley and Jetz 2007), with significant implications for energy partitioning and ecosystem dynamics. Still, along elevational gradients, lizard diversity and abundance decline with increasing elevation, leading to higher predation pressure in lowland habitats (Fu et al. 2007). On islands, the reduced availability of arthropods often results in a shift toward herbivory in lizards

4.5. Ants

Ants contribute substantially to global animal biomass and they are critical ecosystem engineers 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 (Philpott and Armbrecht 2006, Mestre et al. 2012, Mestre et al. 2016). 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 (Rommel and Tammaru 2009), which might have relatively smaller impact on lower

trophic levels (i.e. smaller herbivores cause smaller damage). Very often, the effect of ants on herbivory is skewed due to their interactions with sapsucking arthropods, or due to effect on other predatory arthropods. We for example showed, that ants typically push spiders away (Supriya et al. 2019). Other arthropods may change their behaviour in the presence of ants. For example, beetles may change their walking speed, duration of stops, and walking trajectories in the presence of ants (Reznikova and Dorosheva 2004).

Along elevational gradients, ant species richness either declines or peaks at mid-elevations (Brühl et al. 1999, Colwell et al. 2016). Their ability to fly or float facilitates colonization of islands, where some species achieve extremely high population densities (Morrison 2016). However, predicting their net impact on herbivory is challenging, given their complex interactions across environmental gradients and the variability in their ecological roles (Wiescher et al. 2012). Our review revealed, that ants are manipulated in many enclosure experiments (Sam et al. 2022c), and we ourselves removed them effectively from foliage of understory trees and found rather weak effects of their absence on lower trophic levels (Sam et al. 2023, Sivault et al. 2024b), despite the predation rates caused them were typically high (Sam et al. 2015a, Mrazova and Sam 2019)

4.6. Spiders

Spiders, the seventh most diverse order of animals, are among the most abundant generalist predators in terrestrial ecosystems (Greenstone and Hunt 1993, Riechert et al. 1999, Sunderland 1999, Nyffeler 2000, Symondson et al. 2002). They play a significant role in structuring food-webs, preying on and limiting arthropods (Wise 1995, Halaj et al. 2000, Michalko 2019) and being food to birds (Gunnarsson 1996). Spiders have been shown to have ecosystem-wide impact and can indirectly influence plant community composition, plant matter decomposition and mineralization via consumptive and non-consumptive effects on arthropods (i.e. direct and indirect trophic interaction; (Schmitz et al. 2010, Strickland et al. 2013). In a meta-analysis of experimental studies on the effect of spiders on agricultural pests, spiders generally decreased abundances of pests and improved crop performance (Michalko 2019). However, most research investigating the effects of spiders on plants has focused on plant damage or biomass loss caused by herbivores, without considering that spiders also prey heavily on pollinators (e.g., Morse 1986). Almost all spiders are carnivores that capture predominantly insects and other spiders (Michalko 2019). However, spiders use a wide variety of hunting strategies for diverse prey types, resulting in different trait-mediated effects on their prey (Schmitz et al. 2010, Michalko and Pekár 2016). The functional composition of a spider community with respect to hunting strategies and prey size (Sanders et al. 2015) can influence niche complementarity and consequently predation pressure on arthropods (Michalko 2019). Spiders partition prey resources with vertebrates and may act as both predators and prey within ecosystems (Finke and Denno 2005). Unlike other taxa, spider body size and abundance do not exhibit consistent trends along elevational gradients (Houska Tahadlova et

al. 2022). Their impact on herbivory is influenced by their role as intraguild predators and their interactions with other trophic levels. Studies on spiders along elevational gradients, particularly on islands, are limited, leaving many questions unanswered. In this thesis, we focus on the spiders as on mesopredators in all studies in which we exclude the predators (Houska Tahadlova et al. 2022, Sam et al. 2023, Sivault et al. 2024a, Sivault et al. 2024b).

5. Concluding remarks and future perspectives

This habilitation thesis, I have discussed the definition, importance and spatial diversity in the predation within tri-trophic interactions between plants, arthropods and insectivorous predators. I particularly focused on top-down forces exerted by predators on arthropods, and their cascading effects on herbivory, plant defences, and broader ecosystem functions. I have also addressed the detection of prey by predators, communication between plants and predators, and different types of predators. Despite significant advancements, several research gaps and opportunities remain. Future studies could address the following topics:

1. **Role of multi-predator interactions in shaping food webs:** While this thesis has examined the mostly individual roles of specific predator groups (e.g., birds, bats, ants), future research could investigate more extensively how interactions among multiple predator groups influence prey suppression and herbivory reduction, especially with the respect to the impact on the mesopredators. For example, do synergistic effects among birds, bats, and ants enhance their top-down control on herbivores in all environments? Do they affect the smaller predators to the same extent? There are some indications that spiders and ants have especially complex relationships with respect to the effect on lower trophic levels – mainly due to mutualistic interactions of ants with aphids, spiders including significant amounts of aphids in their prey, and overall competition between ants and spiders, both of them being eaten by birds at the same time.
2. **Impact of non-lethal predator effects (across gradients):** The behavioural changes in prey due to predator presence (fear effects) have cascading impacts on herbivory and plant fitness. However, the extent and variability of these non-lethal effects across elevational, latitudinal, and vertical gradients remain poorly understood. The lack of experiments, even on a smaller scale, is preventing conclusions as we do not know typically anything about how often, how far, and how intensely a predator should be to cause some significant changes in prey feeding behaviour. To my knowledge, this topic is more often studied in aquatic, than in terrestrial environments. Future studies should also examine how prey behavioural shifts vary across gradients, how human activities in the ecosystem affect them and what are the implications of non-lethal effects of predators for forest dynamics – in larger scales.

3. **Predator-prey dynamics in urban, agricultural and fragmented landscapes:** Urbanization, agricultural practices and habitat fragmentation present unique challenges and opportunities for studying trophic interactions. Understanding how predator-prey dynamics are altered in urban or agricultural settings, particularly with the proliferation of generalist predators, could inform agriculture and urban planning. Human activities affect all trophic levels in different ways – by adding nutrients to soils which could affect bottom-up forces as well as by the direct effect on the abundance and richness of predators and/or prey. As these impacts can go in different directions, results on plant herbivory might be difficult to predict, yet they are important for management of the human-altered habitats.
4. **Microbiome-mediated effects of predation:** Gut microbiomes of predators are increasingly recognized as key mediators of their health, diet, and ecological roles. Investigating how the diet diversity of predators influences their gut microbiome, and, in turn, their predation efficiency, could offer novel insights into predator-prey interactions. Disruptions or imbalance to trophic interactions, whether due to habitat loss, climate change, or other factors, may lead to significant shifts in available prey. These changes in diet could directly impact the gut microbiome, potentially reducing the health and fitness of predators. Diminished or imbalanced gut microbiome might impair nutrient absorption, immune response, or even cognitive function, all of which are critical for successful hunting and survival. Moreover, such changes could affect the predators' reproductive success, as poor health and reduced energy reserves may hinder their ability to raise offspring. Understanding these links could have profound implications for predicting and mitigating the effects of environmental changes on predator populations.
5. **Role of evolutionary history in shaping trophic interactions:** More comparative studies across ecosystems with different evolutionary histories could improve our understanding of the influence of co-evolutionary dynamics on predator-prey-plant interactions. For instance, it could be more experimentally and precisely tested whether the tropical ecosystems exhibit stronger or more complex trophic cascades compared to temperate ecosystems. There are many methodological issues, which prevent robust conclusions so far. First of all, primary producers differ significantly between the sites distributed along the latitudinal gradient. Second, standardized methodologies are typically difficult to conduct at places which are located in very different environments far away.
6. **Implications of climate change on predator-prey dynamics:** The effects of climate change, including shifts in temperature, precipitation, and seasonality, are likely to influence predator and prey distributions, behaviours, and interactions. Experimental studies conducted in different settings, with different climatic conditions, or with altered climatic conditions, are needed to predict how these changes will impact trophic interactions and ecosystem stability. It would be advisable to study trophic interactions at places with more extreme conditions,

affected by climate change, e.g. at places threatened by flooding, droughts or unexpected frosts or disrupted regimes of rainy and dry seasons.

7. **Unresolved peculiarities of the use of olfaction for search for prey in predators:** In recent years, many studies showing the unexpected roles of plant volatiles and use of olfactory in the predators during their feeding behaviour. Despite the research effort, there are still many unknown factors – specifically with respect to olfactory use in insectivorous birds, and also in actively hunting predators. Many equivocal results exist too, with some studies failing to conduct the complicated behavioural experiments in these complex systems successfully. Indeed, work with live animals, when we try to investigate what they think and how they perceive certain stimuli, is always difficult. Even more, when the stimuli are very specific to other species and to environmental conditions. Therefore, it is important to combine behavioural approaches together with physiological and ecological parameters.

In conclusion, this thesis underscores the critical role of predators in maintaining terrestrial ecosystem structure and function. Addressing the above-mentioned research directions will not only enhance our understanding of trophic interactions but also provide crucial insights for biodiversity conservation and ecosystem management in the face of global environmental changes.

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7. Summary of articles included in the thesis

This habilitation thesis comprises a portion of my scientific accomplishments focused on the various aspects of predation, and to topics related to trophic interactions between plants, herbivorous arthropods and their predators. These include 19 primary research papers, 2 reviews, 1 book chapter, 1 preprint and 1 manuscript. The papers are all included as appendices to the thesis. The research papers are arranged by the year of publication.

Table 1. List of the studies (number of studies corresponds to the list below) with indications of what methodology was used in them and which factors were investigated. Superscript Rev indicated reviews, BCh stands for a reviewed book chapter, Mn for a manuscript and Prep for a preprint.

Study	Plant-predator communication/behaviour	Dummy predation	Predator survey	Elevation	Predator exclosure	Other factors surveyed
1	Yes	Yes	Yes	Yes		
2		Yes				
3	Yes	Yes	Yes	Yes		
4		Yes				
5			Yes			
6		Yes		Yes		Latitude
7	Yes	Yes				
8			Yes			
9 ^{Rev}	Yes	Yes				
10	Yes	Yes		Yes		
11 ^{Rev}	Yes				Yes	
12			Yes	Yes		
13	Yes	Yes		Yes		Latitude
14				Yes		Herbivory
15	Yes					
16			Yes	Yes		
17			Yes	Yes	Yes	
18	Yes					Non-lethal effect
19				Yes	Yes	Forest type
20	Yes	Yes				
21			Yes		Yes	Vertical strata
22 ^{BCh}				Yes	Yes	
23			Yes	Yes	Yes	
24 ^{Prep}				Yes	Yes	Latitude
25 ^{Man}					Yes	Nutrient addition

- 1) **Tvardikova, K.**, & Novotny, V. (2012). Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. **Journal of Tropical Ecology**, 28(4), 331-341. *The paper originating from research conducted during my Ph.D. stay in Papua New Guinea, in which I show that rolling caterpillars have higher chances for survival than those exposed on foliage, due to lower detection rates by birds in tropical forest understories.*
- 2) Low, P. A., **Sam, K.**, McArthur, C., Posa, M. R. C., & Hochuli, D. F. (2014). Determining predator identity from attack marks left in model caterpillars: guidelines for best practice. **Entomologia Experimentalis et Applicata**, 152(2), 120-126. *A fruitful collaboration during my postdoctoral stay in Australia, where we established a good practice protocol for identification of predation marks on dummy prey and publish an identification guide.*
- 3) **Sam, K.**, Koane, B., & Novotny, V. (2015). Herbivore damage increases avian and ant predation of caterpillars on trees along a complete elevational forest gradient in Papua New Guinea. **Ecography**, 38(3), 293-300. *Using dummy prey on foliage in tropical forest understories, I estimated the predation rate on dummy prey (i.e., caterpillars) and the effect of visual cues to it. I conducted the research along a complete forest elevational gradient, ranging from 200 to 3700 m, focusing on the elevational pattern in predation by different predators as well.*
- 4) **Sam, K.**, Rimmel, T., & Molleman, F. (2015). Material affects attack rates on dummy caterpillars in tropical forest where arthropod predators dominate: an experiment using clay and dough dummies with green colourants on various plant species. **Entomologia Experimentalis et Applicata**, 157(3), 317-324. *Using dummy prey once again, we tested the effect of various materials on the resulting estimates of the predation rate. An important aspect of this study is that we included direct comparison of the predation on the real vs. dummy prey caterpillars.*
- 5) **Sam, K.**, Koane, B., Jeppy, S., Sykorova, J., & Novotny, V. (2017). Diet of land birds along an elevational gradient in Papua New Guinea. **Scientific Reports**, 7(1), 44018. *Along the elevational gradient of Mt. Wilhelm in Papua New Guinea, I investigated the feeding*

patterns of bird species. I identified elevational clines in the diet size as well as changes in the diet preferences. This work was later crucial for other experimental manipulations of bird presence along the gradient.

- 6) Roslin, T., Hardwick, B., Novotny, V., Petry, W. K., Andrew, N. R., Asmus, A., ... **Sam, K.** ... & Slade, E. M. (2017). Higher predation risk for insect prey at low latitudes and elevations. **Science**, 356(6339), 742-744. *Into this highly collaborative study, I contributed significantly by design of the methodology and field work at three study sites. The study describes elevational as well as latitudinal pattern in predation rate on dummy prey. It specifically reports much higher predation rate by arthropods in the tropical regions than in temperate regions, with no change in the latitudinal pattern of predation by birds.*

- 7) Mrazova, A., & **Sam, K.** (2018). Application of methyl jasmonate to grey willow (*Salix cinerea*) attracts insectivorous birds in nature. **Arthropod-Plant Interactions**, 12(1), 1-8. *Together with my Ph.D. student, we investigated whether the application of plant hormone methyl jasmonate would lead to attraction of predators to treated trees in natural conditions. We confirmed that induced plant defences can indeed attract insectivorous predators, and that there is a close relationship between plants and predators.*

- 8) **Sam, K.**, Koane, B., Bardos, D. C., Jeppy, S., & Novotny, V. (2019). Species richness of birds along a complete rain forest elevational gradient in the tropics: Habitat complexity and food resources matter. **Journal of Biogeography**, 46(2), 279-290. *This work represents a very first survey of bird communities along the elevational gradient of Mt. Wilhelm in Papua New Guinea. As such, this work represents crucial background data on the bird communities and on the different feeding strategies. Together with Sam et al. 2017 (publication no. 5 in this list), it represents an important survey of what predation pressure the birds can express along the elevational gradient, and mainly what habitat characteristics affect which feeding guilds. We show that insectivorous birds, more than other guilds are linked to habitat structure and foliage density, which goes in line with the abundance of the arthropods.*

- 9) Mrazova, A., **Sam, K.**, & Amo, L. (2019). What do we know about birds' use of plant volatile cues in tritrophic interactions? **Current opinion in insect science**, 32, 131-136. *This review, which I wrote with my Ph.D. student AM and our colleague LA (with whom AM undergo her foreign Ph.D. stay), evaluates the role of birds in relation to the 'crying for help' hypothesis and their use of olfactory cues. The study is a reaction to an earlier review, after which many new papers with contradictory findings appeared, and we thus provided a more critical opinion on the topic.*
- 10) Mrazova, A., & **Sam, K.** (2019). Exogenous application of methyl jasmonate to *Ficus hahliana* attracts predators of insects along an altitudinal gradient in Papua New Guinea. **Journal of Tropical Ecology**, 35(4), 157-164. *Together with my Ph.D. student, we once again investigated whether the application of plant hormone methyl jasmonate would lead to attraction of predators to treated trees, this time in the natural conditions of tropical forest understories. We again confirmed that induced plant defences can indeed attract insectivorous predators, and that there is close relationship between plants and predators. Yet, this time, ants seemed to play a role of significant predators being attracted to the treated trees. This research was conducted at several sites along the elevational gradient, providing further insights into the mechanisms of the interactions between plants and predators across various habitats.*
- 11) Singer, M., **Sam, K.**, & Rodríguez-Castañeda, G. (2019). Editorial overview: Communication in multitrophic interactions - new analytical approaches and emerging ecological consequences. **Current opinion in insect science**, 32, 3-5. *A short review to introduce the special issue we organized for the journal together with my colleagues.*
- 12) **Sam, K.**, & Koane, B. (2020). Biomass, abundances, and abundance and geographical range size relationship of birds along a rainforest elevational gradient in Papua New Guinea. **PeerJ**, 8, e9727. *During my work along elevational gradient, I spotted that some montane bird species are unexpectedly more common and recorded more often than typical birds in lowlands, potentially thus causing stronger predation pressure on prey. I later on realized that similar patterns are not typical and have been described so far only from Africa. Specifically, our results showed that montane bird species maintain dense populations which compensate for the reduced available area near the top of the mountain.*

- 13) Valdés-Correcher, E., Moreira, X., Augusto, L., Barbaro, L., Bouget, C., Bouriaud, O., ... **Sam, K.** ... & Castagneyrol, B. (2021). Search for top-down and bottom-up drivers of latitudinal trends in insect herbivory in oak trees in Europe. **Global Ecology and Biogeography**, 30(3), 651-665. *As a partner to this larger consortium focusing on the multitrophic interactions associated with oaks, we focused on the relative importance of bottom and top-down forces affecting herbivores and herbivory damage on oaks across the latitudinal gradient of their distribution. I managed two study sites by myself, and two of my other students contributed data from two additional sites within the Czech Republic.*
- 14) **Sam, K.**, Koane, B., Sam, L., Mrazova, A., Segar, S., Volf, M., ... & Novotny, V. (2020). Insect herbivory and herbivores of *Ficus* species along a rain forest elevational gradient in Papua New Guinea. **Biotropica**, 52(2), 263-276. *In this paper, we tested the classic hypothesis that plant-herbivore interactions are stronger, and herbivory thus higher, under warmer conditions. As I believed that this view might be oversimplified, we investigated both arthropod communities, herbivory damage they cause, as well as plant defences (i.e. bottom-up forces). We described that herbivore damage and herbivore abundances varied significantly with elevation (following a hump-shaped pattern), as well as among the tree species, and between the wet and dry seasons.*
- 15) **Sam, K.**, Kovarova, E., Freiberga, I., Uthe, H., Weinhold, A., Jorge, L. R., & Sreekar, R. (2021). Great tits (*Parus major*) flexibly learn that herbivore-induced plant volatiles indicate prey location: An experimental evidence with two tree species. **Ecology and evolution**, 11(16), 10917-10925. *In this experiment with naïve young birds, we tested whether birds are capable of flexibly learning various herbivore induced plant volatiles (HIPV) and associate them with moments when they obtained the food. After several such positive associations, they were able to navigate to odour directly, without the need to see the real food. We demonstrate that the ability to learn to associate HIPVs with food reward is flexible, expressed for both tested plant species, even if the plant species has not coevolved with the bird species (i.e., guava). Our results imply that the birds are not capable of generalizing HIPVs among tree species but suggest that they either learn to detect individual compounds or associate whole bouquets with food rewards.*

- 16) 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(1), 81-94. *In this study, my Ph.D. student ES investigated communities of bats along the elevational gradient of Mt. Wilhelm (same sites as in studies no. 8 and 14), bringing thus very novel data about the distribution of bats and their feeding strategies, which will be further used in other studies.*
- 17) **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. *This study represents a very first large and extensive study, during which I excluded predators in a factorial design along the elevational gradient. Specifically, I excluded flying vertebrate predators and ants individually and in combination, from more than 600 small trees growing at 8 study sites spanning elevations from 200 to 3700 m asl. We showed that while the effect of ant exclusion was rather weak and did not lead to changes in plant herbivory, the effects of the exclusion of vertebrate predators were strong, and stronger in the wet season than in the dry season.*
- 18) Kollross, J., Jancuchova-Laskova, J., Kleckova, I., Freiberga, I., Kodrik, D., & **Sam, K.** (2023). Nonlethal Effects of Predation: The Presence of insectivorous birds (*Parus major*) affects the behavior and level of stress in locusts (*Schistocerca gregaria*). **Journal of Insect Behavior**, 36(1), 68-80. *Together with my Ph.D. student JK, we investigated the feeding activity of insects (time spent by feeding and willingness to reach food) which is under the stress from the presence of predators. We tested how fast the stress can be detected hormonally in the haemolymph and in central nervous system, which distances from predators induce the stress, and whether the real presence of a predator is needed, or whether the sound of a predator is sufficient to induce the stress.*
- 19) Houska Tahadlova, M., Mottl, O., Jorge, L. R., Koane, B., Novotny, V., & **Sam, K.** (2023). Trophic cascades in tropical rainforests: Effects of vertebrate predator exclusion on arthropods and plants in Papua New Guinea. **Biotropica**, 55(1), 70-80. *Together with my Ph.D. student MHT, we conducted exclosures of flying predators in different forest types and at two different elevations, in tropical Papua New Guinea. We showed no strong*

differences between the forest types, but rather a consistent effect of predators on lower trophic levels, both on arthropod communities and herbivory damage.

- 20) Mrazova, A., Houska Tahadlova, M., Rehova, V., & **Sam, K.** (2023). The specificity of induced chemical defence of two oak species affects differently arthropod herbivores and arthropod and bird predation. **Arthropod-Plant Interactions**, 17(2), 141-155. *Together with my Ph.D. student AM, and her bachelor student VR, we conducted an experiment with two oak species, on which we measured the predation pressure, under control and induced conditions. Specifically, we induced volatile compounds by methyl jasmonate and observed whether the induced trees will be more attractive to various predators. We further investigated the differences in the chemical compounds induced by the two oak species. We confirmed that induction of volatile compounds by the methyl jasmonate is possible on both species, and the birds indeed arrive more often to the potentially more herbivore rich plants.*
- 21) Sivault, E., Kollross, J., Jorge, L. R., Finnie, S., Diez-Méndez, D., Fernandez Garzon, S., ... & **Sam, K.** (2024). Insectivorous birds and bats outperform ants in the top-down regulation of arthropods across strata of a Japanese temperate forest. **Journal of Animal Ecology**, 93(11), 1622-1638. *This study represents a core of my current research and the first methodological paper where we describe how to exclude predators in a factorial design. In temperate Japanese forest, we worked both in forest understory and canopy, and we excluded birds and bats individually, and flying vertebrates and ants in combinations. We accompanied our research with the survey of all involved predators. Contrary to our original hypotheses, we found a similar effect of predators in forest understory and in canopy, and along with our expectation, we found a very weak effect of ants. To our surprise, we observed an equal importance of bats and birds in the system, and a rather antagonistic relationship between birds, bats and ants.*
- 22) **Sam, K.**, Mrazova, A., Houska Tahadlova, M., Kollross, J., & Maraia, H. (2024). Impact of predators on arthropod herbivores and herbivory along mountain ranges on islands versus mainland. In *Ecology and Evolution of Plant-Herbivore Interactions on Islands* (pp. 199-217). Cham: Springer International Publishing. *In this book chapter, we reviewed and summarized the results of all existing studies in which flying vertebrates vs. ants have been excluded on mainland vs. on islands, at different elevations. Our findings indicate that*

insectivorous vertebrates significantly reduce arthropod abundances and herbivore damage. This effect was stronger overall on islands than on mainland but did not vary significantly with elevation for either landform type. In contrast, the mean effects of invertebrate predators, i.e., ants, on herbivory did not differ between mainland and islands (though significant increases in herbivores and herbivory were found on mainland but not islands), but did show a significant decrease with elevation which was statistically indistinguishable across landform types.

- 23) Sivault, E., Koane, B., Chmurova, L., & **Sam, K.** (2024). Birds and bats reduce herbivory damage in Papua New Guinean highland forests. **Ecology**, 105(11), e4421. *While returning to the elevational gradient of Mt. Wilhelm with my Ph.D. student ES, we conducted a set of predator exclosures, this time focusing on the effect of elevation on the importance of bats and birds individually. By working on four elevations and manipulating the presence and absence of the birds and bats in diurnal exclosures, we showed unexpectedly high importance of the bats, which was typically similar or even higher at some places, than the importance of the birds. In the study, similarly as in others, we investigated the effect of the absence of the predators on insect communities as well as on herbivory damage.*
- 24) **Sam, K.**, Tahadlova, M., Freiberga, I., Mrazova, A., Toszogyova, A., & Sreekar, R. (2022). The impact of ants and vertebrate predators on arthropods and plants: a meta-analysis. **Manuscript at bioRxiv**, 2022-06. *With my team, we collected data from all exclosure experiments conducted so far, and conducted an analysis of them, linking the effect of predators (flying vertebrates vs. ants) to latitude, elevation and productivity (NDVI respectively). We found a rather globally robust effect of flying vertebrates and a small effect of ants, which was however stronger in lowlands. Altogether, we are pointing out various methodological issues, suggesting good practices, length of the exclosures and appropriate sizes of the exclosures. The manuscript was submitted to Ecology, currently pending our major revision.*
- 25) Kollross, J., Jorge, L. R., **Sam, K.** Impact of predator exclusion and nutrient enrichment on arthropods and herbivory damage. **Manuscript**. *In this manuscript, together with my Ph.D. student JK, we tested the effect of nutrient addition (N, P, K) on the leaf traits and herbivory of temperate trees, in the absence vs. presence of flying vertebrates. We found a relatively*

stronger effect of nutrient addition on the leaf herbivory damage, than the presence of predators. We thus confirmed the hypothesis that bottom-up forces shape the tri-trophic interactions. Effect of predator exclusion were less pronounced, potentially due to larger predatory arthropods (i.e., spiders) compensating for the absence of flying vertebrate predators.

8. Attached publications

The following is an attachment of print publications.