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Ecological trends in geometrid moth communities along elevational gradients in tropical rainforests with lessons for tropical biodiversity conservation

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Ecological trends in geometrid moth communities along elevational gradients in tropical rainforests with lessons for tropical biodiversity conservation

Ph.D. Thesis

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❖ **Annotation**

The present thesis focuses on the larger theme of the composition of highly diverse insect communities in tropical rainforests, using geometrid moths (Lepidoptera, Geometridae) as a model taxon. In particular, the study examines the structure and alpha diversity of moth communities at different elevations, their beta diversity as their composition responds to ecological trends in elevation gradients, and their regional gamma diversity as two elevation gradients with a separate geological history are compared and analyzed together. First, we examined changes in geometrid community composition along one of the few complete rainforest elevation gradients in the Palaeotropics, spanning from the lowlands to the timberline at 3700 m asl at Mt. Wilhelm. This is a well-studied gradient to explore a range of drivers of community composition along elevational gradients, including climate, the composition of vegetation, and the predation pressure. We used the same sampling protocols along a shorter elevation gradient in the Whiteman Range on the island of New Britain, which is geographically close, but being an oceanic island, it does not have a common geological history with Mt. Wilhelm. This allowed us to examine species turnover between two gradients and local endemism. Finally, the experience with ecological research in Papua New Guinea, in combination with the thesis author coming from an indigenous community of rainforest landowners, led to the examination of the current situation and future trends in rainforest conservation by indigenous communities globally, and particularly in Papua New Guinea.

❖ Declaration

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

České Budějovice, 6th of November, 2023

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Pagi S. Toko

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

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❖ List of papers, manuscripts and author's contributions

The thesis is based on the following papers and manuscripts:

Chapter I

Toko, P. S., Koane, B., Molem, K., Miller, S. E. & Novotny, V. (2023) Ecological trends in moth communities (Geometridae, Lepidoptera) along a complete rainforest elevation gradient in Papua New Guinea. *Insect Conservation and Diversity* **16**, *649-657* (impact factor: 3.5). https://doi.org/10.1111/icad.12663

Personal contribution: Field work (100%); Conceptualization (50%); Data analysis (60%); Species identifications (60%); Literature review (100%); Preparation of figures and tables (100%); Writing manuscript (90%).

Chapter II

Toko, P. S., Lilip, R., Ibalim, S., Amick, P. K., Miller, S. E. & Novotny, V. Composition and structure of rainforest moth (Geometridae, Lepidoptera) communities along an island elevational gradient in New Britain (Papua New Guinea). (Manuscript)

Personal contribution: Fielwork (50%); Conceptualization (100%); Data analysis (80%); Species (100%); Literature review (100%); Preparation of figures and tables (100%); Writing manuscript (90%).
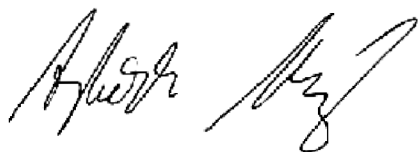
Chapter III

Toko, P. S., Dem, F., Cámara-Leret, R., Martins, D. J., Philip, J., Matapi, U., West, P. & Novotny, V. Biodiversity conservation with Indigenous peoples in tropics. (Manuscript submitted to *Nature*, a revision requested)

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❖ **Co-author agreement**

Vojtěch Novotný, the sole supervisor of this Ph.D thesis and the senior author in chapters I, II & III, fully acknowledges the major contribution of Pagi S. Toko to these manuscripts.

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Prof RNDr. Vojtěch Novotný, CSc.

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GENERAL INTRODUCTION

Ecological trends in geometrid moth communities along elevational gradients in tropical rainforests with lessons for tropical biodiversity conservation

Ecological trends in geometrid moth communities along elevational gradients in tropical rainforests with lessons for tropical biodiversity conservation.

INTRODUCTION

Tropical biodiversity: alpha, beta and gamma

Tropical rainforests are by far the most biodiverse biome on earth. There are many interacting reasons why tropical rainforests are so diverse compared to the other world's biomes. These drivers include historical phylogenetic processes leading to high diversification rate in the tropics, as well as contemporary abiotic conditions, including high energy input and climate predictability, as well as biotic condition including bottom-up and top-down control of population dynamics (Hill & Hill, 2001; Wilson, 1988).

Presently, the Neotropical forests in the Amazon, the Congo Basin in Africa and the island of New Guinea in the Indo-Pacific region are the three largest blocks of rainforest (Cámara-Leret et al., 2020; Slik et al., 2015; Valencia et al., 1994). The tropical rainforests are home to a majority of insect species, whose global diversity is variously estimated between 4 and 30 million species (Erwin, 1982; Novotny et al., 2006). This insect diversity is primarily tied to a high diversity of vegetation. There are 40-53,000 tropical tree species serving as resource base for herbivorous insects that support further trophic levels of insect predators and especially parasitoids (Slik et al. 2015, Basset et al., 2012; Novotny et al., 2007).

On the local, community level, the tropical tree diversity is also remarkable, as tropical rainforests reach 300 – 1000 species of woody plants per 50ha, the largest standard plot size used for tropical inventories (Anderson-Teixeira et al., 2015). This diversity, alongside with large diversity of epiphytes, lianas, and herbaceous plants (e.g., Cámara-Leret et

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al., 2020) host the estimated 10,000 herbivorous species from various insect guilds in a single community, engaged in ~40,000 distinct plant-herbivore interactions (Novotny et al. 2010) and with still unknown numbers of insect species in the upper trophic levels of predators and parasitoids.

Long elevational transects in humid tropics represent a global biodiversity maximum on the landscape level, connecting the community and continental spatial scales (Rahbek et al. 2019). Tropical rainforest gradients span from large lowlands to the timberline at 3,500 – 4,000 m asl, with rapid species turnover driven by strong ecological gradients in abiotic and biotic variables (Beck et al. 2017, Colwell et al. 2016, Kessler, 2002; McCain, 2005, 2009). Elevation gradients are also "natural laboratories" for ecologists to study species diversity and abundance with respect to biotic and abiotic environmental factors and their change, including recent concerns about climate change (Pounds et al. 2006).

Over the past 50 years, tropical rainforests have come under immense pressure, initially largely from commercial logging but presently particularly from land conversion to agriculture (Laurance et al., 2001, 2011; Shearman et al., 2009). The deforestation in rainforests threatens global biodiversity, as well as ecosystem function and therefore ecosystem services provided by tropical forests (Watson et al. 2016, Gardner 2009, Dirzo et al. 2014). Rainforest conservation is a complicated problem combining biological, economic, and political factors. One important, but often unappreciated or misrepresented, factor is the role of indigenous peoples living in rainforests in their preservation (Novotny 2010). Indigenous peoples have shaped rainforest ecosystems for thousands of years (Ellis et al. 2021) and at present they exert very variable degree of control over their fate, from being displaced to being legally recognized landowners. The latter is the case in Papua New Guinea, providing thus an excellent "social laboratory" for indigenous rainforest conservation (Novera & Kark, 2022).

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Elevational gradients as biodiversity hotspots

The interest in elevational gradients dates back to the origins of biogeography, particularly to Alexander von Humboldt who laid the foundation of the modern concept of elevation zones along elevation gradients (Lomolino, 2001; Von Humboldt & Bonpland, 2010). The ecology of elevational gradients also influenced early works by Joseph Grinnell and Robert H. MacArthur as they were instrumental in clarifying the concepts of niches, species coexistence, and community assembly from regional species pools (Holdridge, 1947; Grytnes & McCain, 2007). The studies along elevation gradients have also contributed to our understanding of alpha and beta diversity patterns (Colwell et al., 2004; Grytnes & McCain, 2007; Lomolino, 2001) and more recently they have become experimental ecosystems for the study of climate change impacts (Pounds et al., 1999; Chen et al., 2009; Gore, 2006). Tropical species are likely to expand or shift their distribution ranges towards higher elevations, in line with approximately 5.4°C decrease in mean annual temperature for every 1000 elevation meters (Chen et al., 2011). However, the survival of lowland species, often near their physiological temperature limits, under global warming is a matter of discussion (Colwell et al. 2004); will there be a large-scale species attrition in warming tropical lowlands? To complicate matters, elevational changes in species distribution could generate new pathogen-host combinations such as for chytrid fungi threatening amphibian diversity (Pounds et al., 2006; Blaustein & Dobson, 2006), as well as disrupt the existing trophic interactions. In addition to being possible avenues for species to adjust their distribution to changing climates, elevation gradients already concentrate disproportionate numbers of plant and animal species relative to their land area (Rahbek et al., 2019; Barthlott et al., 1996). These species are often endemic, making tropical mountains prime targets for biodiversity conservation (Rahbek et al., 2019).

Drivers of species diversity patterns along elevational gradients

Species diversity along elevational gradients shows two most common patterns: (1) monotonous decrease with increasing elevation, or (2) mid-elevational peak. The drivers behind these patterns may be numerous and complicated. The favourability of climatic conditions, particularly temperature, decreases with increasing elevation. However, the decreasing abiotic favourability and habitat area with increasing elevation may be compensated by increasing biotic favourability, as predation and pathogen pressure tends to decrease with increasing elevation (Roslin et al. 2017, Sam et al. 2017). The two opposing trends could generate a mid-elevation maximum in species diversity. However, a similar maximum could also arise due to mid-domain effect, by mixing low- and high-elevation species (Lomolino 2001, Colwell et al. 2016).

There is a general decrease in land area with increasing elevation. Within the rainforest biome, the <100 m asl. area is larger than the area of all higher elevations combined; the alpine habitats are particularly small (Rahbek et al. 2019). The species-area relationship (SAR) alone should explain a large portion of monotonous decline of diversity with elevation, although quantitative tests are rarely attempted (Rosenzweig, 1995).

The importance of elevation gradient in temperature may be particularly high for insects as it determines their metabolic rates, as well as the rate of development and therefore the number of generations per year (Allen et al., 2007). Elevation gradients in temperature affect insects also indirectly, via its impact on vegetation. In some analyses of insect communities, including geometrid communities, temperature was one of the leading predictors of their diversity and other community parameters (Brehm et al., 2003a, 2003b).

Rainforest net primary productivity, plant standing biomass and plant species richness can be either decreasing monotonously with decreasing temperature or have a mid-elevation maximum (Taylor et al. 2017, Mittelbach 2001). However, these parameters are not necessarily

correlated so that some of them can exhibit a monotonous decline while others a mid-elevation gradient along the same elevation gradient (Girardin et al. 2014). High biomass and diversity of plants create complex habitats for insects and provide them with abundant and diversified food resources, but insect communities use these resources unevenly as herbivore load of individual plant species widely varies (Novotny et al. 2010).

The Mid Domain Effect is a null model proposed to explain species diversity along elevational gradients based on geometric constraints of species distributions along gradients (Colwell et al. 2004, 2016, Gotelli & Graves, 1996). A random allocation of species' elevation ranges along an elevation transect leads to a mid-elevation maximum where the ranges of the largest number of species overlap. The explanatory power of MDE remains disputed (Dunn et al., 2007, Hawkins et al., 2005; Hawkins & Diniz-Filho, 2002) as this mechanism is difficult to separate from the effects of other environmental drivers producing mid-elevation species diversity maximum, observed for instance for geometrid moths (Beck et al., 2017), ferns (Kessler et al., 2011), or amphibians (Fu et al., 2006; Hu et al., 2011).

The biotic interactions including competition, predation, mutualism and parasitism all exhibit elevation trends (Choler et al., 2001; Sam et al., 2017, 2023; Tahadlova et al., 2022). For instance, there is a global trend of decreasing predation risk with increasing elevation (Roslin et al., 2017). The ant-plant and ant-homopteran mutualisms will also decrease with elevation, following a decline in ant abundance and diversity (Plowman et al., 2017, Moses et al. 2021). Insectivorous birds and bats, as major groups of insect predators, decline in diversity and abundance with increasing elevation (Sam et al. 2019, Sivault et al. 2023).

The analysis of relative importance of these factors for elevation gradients in diversity, abundance and species composition in communities is a major challenge as many factors display parallel elevational trends (e.g., temperature and land area), some are difficult to measure (e.g., predation

pressure), and many could act simultaneously, often in opposite directions (e.g., abiotic vs. biotic factors).

Geometrids moths as a model taxon in New Guinea

Geometrid moths are one of the largest families of moths in the world with ~24,000 species. They are almost all herbivorous, with caterpillars feeding externally on a wide range of plant species, and ranging in host specialization from monophagy to broad host plant ranges (Rajaei, 2022). They are relatively well known taxonomically (Holloway, 1987) and can be consistently and efficiently sampled by light trapping (Beck et al., 2017). These traits make them one of the most popular model taxa for the study of tropical communities of insect herbivores. The taxonomic knowledge of geometrids is being supplemented by increasingly resolved phylogenies (Murillo-Ramos et al., 2017) and the COI barcode library in the Barcode of Life Database System (BOLD), a massive global DNA sequencing database available for both scientists and the public (Hebert et al., 2003; Marshall, 2005; Ratnasingham & Hebert, 2013).

New Guinea is the world's floristically most diverse island (Camara-Leret et al., 2020), harbouring one of the three largest blocks of rainforest in the world. It is also one of the few tropical areas with several montane ranges reaching the alpine zone, including also one of only two glaciers in the Palaeotropics. The Mt. Wilhelm – Huon Peninsula region represents one of the six hotspots of vascular plant diversity in the world, when measured within 100x100 km spatial units (Barthlott et al., 1996). It is an ideal place for the study of elevation gradients as it comprises several complete rainforest transects, spanning from undisturbed forest in the lowlands to the timberline. In particular, the Central Range with the highest peak in PNG, Mt. Wilhelm, has been studied already for several plant and animal taxa (Novotny & Toko 2015). Further, there is a geologically younger Finisterre-Saruwaged massif on the Huon Peninsula, as well as lower ranges in the adjacent oceanic islands, including the Whiteman Range on

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the island of New Britain. Despite such suitable setting, the previous elevational studies as well as studies of geometrids in New Guinea have been rather limited, including only a few studies of geometrid communities using light trapping (Hebert, 1980; Orsak et al., 1995). Szent-Ivany compiled a list of geometrids at Wau and Mt Kaini (Gressitt & Nadkarni, 1978), laying foundations for geometrid taxonomy, which however remains poorly resolved.

Tropical rainforest conservation with indigenous peoples

Papua New Guinea is one of the few rainforest areas that could be classified as natural wilderness, with >70% of landscape intact (Mittermeier et al., 2003). In many other tropical countries, ecological research on rainforests is limited to an archipelago of the habitat islands, often surviving as conservation areas. In PNG, the rainforest disturbance has been limited, mostly taking place as slash and burn agriculture or selective logging (Shearman et al., 2009). The traditional land ownership of PNG indigenous population has been fully legally recognized so that the indigenous landowners control access to 97% of land (West, 2006). This situation, together with the insights coming from the present Thesis' author being also a member of an indigenous community, inspired the analysis of the role of indigenous peoples in rainforest conservation. PNG, where indigenous peoples have a relative freedom of action, is an excellent test system for the opportunities and problems of indigenous conservation (Novotny & Toko, 2015). However, it is arguably not representative of the situation of indigenous peoples, and the rainforests, in the remaining tropical areas. The current and potential roles of indigenous peoples therefore need to be evaluated worldwide. Conservation is a political process shaped not only by biological laws but also the attitudes and priorities of people, as well as local and global politics and economy. An insight into indigenous communities is therefore important to evaluate how they could contribute to conservation while also responding to their social, cultural, and economic aspirations. Such analysis is topical since even in

PNG, where indigenous people play an outsize role in conservation, the rainforest conservation has not been particularly successful (Shearman & Bryan 2011, Novotny 2010).

Aims and scope of the Thesis

The present Thesis focuses on the larger theme of the composition of highly diverse insect communities in tropical rainforests, using geometrid moths (Lepidoptera, Geometridae) as a model taxon. The study examines the structure and alpha diversity of moth communities at different elevations, their beta diversity as their composition responds to ecological trends along elevation gradients, and their regional gamma diversity as two elevation gradients with a separate geological history are compared and analyzed together. The experience gained during the field research in collaboration with indigenous rainforest-owning communities is then used to examine the role of indigenous communities in rainforest conservation in PNG and in general.

Chapter I examines changes in geometrid community composition among eight elevations regularly spaced by 500 elevational meters along one of the few complete rainforest elevation gradients in the Palaeotropics, spanning from the lowlands to the timberline at 3700 m asl at Mt. Wilhelm (PNG). This is a well-studied gradient (Novotny & Toko, 2015) allowing to explore a range of drivers of community composition and diversity along elevational gradients, including climate, the composition of vegetation, and the predation pressure.

Chapter II applies the Mt. Wilhelm sampling protocols on a shorter elevation gradient in the Whiteman Range on the island of New Britain, a geographically close oceanic island that does not have a shared geological history with Mt. Wilhelm. This situation made it possible to examine geometrid species turnover between two gradients as well as the degree of local endemism, leading to the assessment of geometrid diversity on the landscape scale.

The experience with ecological research in Papua New Guinea, in combination with the Thesis author being a member of an indigenous community of rainforest landowners, led to **Chapter III** that examines the history, current situation and possible developments in rainforest conservation. While indigenous peoples have lived in most rainforests for centuries, their control over their traditionally owned lands ranges from legally fully recognized, such as in Papua New Guinea, to complete alienation of these lands in many areas of Africa and South America. The review of this situation outlines the paths toward the correlated goals of protecting biodiversity, maintaining traditional cultures, and achieving socioeconomic development in tropical rainforest communities.

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CHAPTER I

Ecological trends in moth communities (Geometridae, Lepidoptera) along a complete rainforest elevation gradient in Papua New Guinea

ORIGINAL ARTICLE

Ecological trends in moth communities (Geometridae, Lepidoptera) along a complete rainforest elevation gradient in Papua New Guinea

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Abstract

1. The tropical rainforest elevation gradients, extending from lowlands to treeline, often represent global maxima of biodiversity and are models for community studies.

2. We surveyed geometrid moths along a complete rainforest gradient from 200 to 3700 m asl. in Papua New Guinea. The 16,424 moths collected with light traps represented 1102 species, a high diversity for such system. We demonstrated the importance of molecular data for taxonomy as COI sequences (DNA barcodes) changed the definition of 19% of morphological species.

3. The abundance of geometrids did not change with elevation while their species richness peaked at 1200 m asl. The mid-elevation diversity peak is a common, but poorly understood, pattern for geometrids. It was best explained by the species richness of the vegetation. At the same time, the community was exposed to opposing trends in abiotic favourability (decreasing temperature) and biotic favourability (decreasing predation by ants, birds and bats) with elevation, potentially contributing to such unimodal trends in species richness.

4. Beta diversity of communities separated by 500 m elevation increased with increasing elevation, reflecting decreasing mean elevational range of species—a pattern opposite to that expected under the Rapoport's rule.

5. The total number of species along the elevation gradient corresponded to 280% of the highest local community diversity. This enrichment of species underscores the key role of long elevational gradients in maintaining high regional diversity and makes them a conservation priority, especially as they also allow for redistribution of species in response to climate change.

KEYWORDS
altitudinal gradient, beta diversity, geometrids, insect herbivory, Melanesia, predation, species diversity, tropics

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INTRODUCTION

Global biodiversity maxima, which include, for example, all six of the world's floristically richest areas hosting >5000 plant species per 10,000 km^2 (Kier et al., 2005), often include long elevation gradients in the humid tropics, particularly the 'complete' rainforest elevation gradients that extend from lowlands to treeline, typically at ~3700 m asl. These gradients encompass a series of highly diverse rainforest ecosystems within a small geographic area, resulting from high species turnover along steep abiotic and biotic ecological gradients. These transects are ideal models for studying the mechanisms of community assembly without complicating effects of dispersal limitation. Recently, they have also become important in climate change research because they reproduce a wide range of temperatures in a limited area.

To a first approximation, species diversity shows either a monotonic decrease with increasing elevation, or a maximum at intermediate elevations (Rahbek, 1995; Stevens, 1992). The monotonic decline in species diversity may be directly or indirectly due to decreasing temperature and/or land area with increasing elevation (Beck & Chey, 2008; Beck & Kitching, 2009). Other important factors include primary productivity and habitat complexity, including vegetation structure important for birds (Sam et al., 2019), or the amount of litter important for ants (Moses et al., 2021; Pérez-Toledo et al., 2021). The maximum diversity at mid-elevation rarely corresponds to a single abiotic or biotic driving variable. It may be a product of the mid-domain effect (Colwell et al., 2016) and/or a combination of multiple factors. In particular, biotic pressures from predators and pathogens tend to decrease and abiotic stress tends to increase with increasing elevation (Péré et al., 2013). Unfortunately, trends in the intensity of trophic interactions such as herbivory, parasitism, or predation are particularly poorly known because they are often caused by multiple taxa that are rarely studied together (Bärtschi et al., 2019; Peters et al., 2016).

Gamma diversity along an entire elevation gradient is a product of alpha diversity values in individual communities and the rate of species turnover across elevations. The Rapoport rule suggests that beta diversity should decrease with increasing elevation, as montane species should have larger elevational ranges than lowland species (Stevens, 1992). However, trends in beta diversity along elevational gradients are studied less often than in alpha diversity (Grytnes & McCain, 2007). Beta diversity along an elevational gradient determines the overall extent of regional, transect-long gamma diversity. For example, a complete rainforest elevational gradient from lowland rainforest to treeline at Mt. Wilhelm in New Guinea included 1.4 to 3.3 times more species than the most species-rich community of that gradient, depending on the plant or animal taxon considered (Novotny & Toko, 2015).

Insects, with their high species richness and diverse ecological functions, have often been used as model taxa to study ecological trends along elevational gradients (Chen et al., 2009; Colwell et al., 2008; McCain, 2009, 2010). Geometrid moths (Geometridae, Lepidoptera) have become a widely used model for insect community studies (Beck et al., 2017) because they are one of the largest, but still taxonomically manageable, insect families, with ~24,000 described species (Rajaei et al., 2022). In addition, adults can be easily surveyed with light traps. Because of their herbivorous lifestyle, geometrids are sensitive to environmental changes, including climate change (Chen et al., 2009), vegetation disturbance (Holloway et al., 1992) and successional dynamics of vegetation (Ashton et al., 2016).

Geometrids generally exhibit maximum diversity at mid-elevations along elevational gradients. However, despite the wealth of available data, the causes of this pattern are not clear (Beck et al., 2017). Here, we study highly diverse geometrid communities along a complete rainforest elevational gradient at Mt. Wilhelm (Papua New Guinea) with the goal of describing and explaining elevational trends in their species composition and alpha and beta diversity and characterising the contribution of elevational gradients to regional gamma diversity. We hypothesise that a unimodal maximum in geometrid species diversity is a composite result of decreasing abiotic environment favourability, particularly decreasing temperature, and increasing biotic favourability, particularly decreasing predation pressure, with increasing elevation. In addition, we also expect a positive correlation of species diversity of mostly herbivorous geometrid moths with the diversity of vegetation that constitutes their resource base. These factors, together with plant species composition, should also explain the species composition of geometrid communities. Finally, we expect increasing beta diversity with increasing elevation as a consequence of Rapoport's rule.

MATERIALS AND METHODS

Study area and vegetation sampling

We studied a complete primary rainforest elevation gradient, from lowlands to timberline, on the slopes of Mt. Wilhelm (4509 m). It is the highest peak in Papua New Guinea and lies in the Central Range, the largest massif on the island of New Guinea and one of the most extensive montane ranges in the humid tropics. The Mt. Wilhelm transect included eight study sites between 200 and 3700 m asl., separated by regular intervals of 500 elevation metres (Figure S1).

Mean annual temperature decreases at a constant rate of 0.54°C per 100 elevation metres from the lowlands at 200 m asl. (27.4°C) to the timberline at 3700 m asl. (8.37°C) on Mt. Wilhelm, based on one-year measurements by data loggers (Sam et al., 2019). Mean annual precipitation ranges from 3300 mm in the lowlands to 4400 mm at the timberline, with a condensation zone at about 2600 m elevation (Sam et al., 2019). The transect is characterised by a mild dry season, typically between June and August.

Vegetation at our study sites was recorded by a census of all stems with a DBH ≥5 cm in three 20 × 20 m primary forest plots at each elevation. Vegetation was characterised by basal area and number of species within the three plots combined at each elevation.

Geometrid sampling and identification

Geometrid moths were sampled in two periods: in the dry season from May to October 2009 at 700, 1700, 2700 and 3700 m asl., and in the wet season from November 2009 to January 2010 at 200, 1200, 2200 and 3200 m asl. We used light sheets with a single 240 W mercury vapour lamp powered by a portable generator. At each site, we sampled for 7–10 nights, depending on weather conditions. The site at 1700 m elevation was sampled twice to examine the effects of a larger sample size. The light sheet was set at a different location each night and operated from 18:00 to 24:00. We have used a different location for each of the minimum seven nights of sampling per elevation, at least 50 m apart from other sampling points. In practice, this means that we typically covered 2 ha of forest by our sampling at each elevation. During this time, all geometrid moths were collected by hand from a 1×2 m white sheet placed in a forest gap or on higher ground so that the light was visible from at least 50 m away. Light trapping is the most commonly used method to survey geometrid communities (Beck et al., 2017). It is an activity-based method that introduces sampling biases depending on species mobility and possibly body size (Holloway, 1987).

The sampled specimens were all sorted into morphospecies based on external morphology using *The Moths of Borneo* (Holloway, 1993, 1996, 1997) as a general guide. From each morphospecies, up to 10 individuals per species were mounted and identified. Each morphospecies was assigned a unique code. In the next step, we collected legs from one to eight individuals per species and elevation, depending on availability, for COI barcoding, using standard Sanger techniques at the Biodiversity Institute of Ontario (Wilson, 2012). BINs, barcode-based molecular species, were integrated with our morphological evidence into final species concepts (Ratnasingham & Hebert, 2013). Data for 1567 sequences classified into 596 BINs are publicly available in the Barcode of Life database (BOLD, data set PAGIB). Most voucher specimens are at the New Guinea Binatang Research Center, PNG, and a synoptic collection is at the National Museum of Natural History, Smithsonian Institution, USA.

Predation pressure analysis

We used existing data on abundance and species diversity of insectivorous bats based on audio surveys (Sivault et al., 2023), insectivorous birds based on point counts (Sam & Koane, 2020), and ants based on tuna baits for abundance and pitfall traps for species diversity (Moses et al., 2021; Sam et al., 2015). All datasets were obtained at our study sites along the Mt. Wilhelm elevation gradient. It is difficult to integrate the impacts of these three predator groups because ants can prey on geometrid caterpillars, birds also prey primarily on caterpillars, while bats prey primarily on adults. We standardised each data set to the range (0, 1) and used the average of the three taxa as an index of predation pressure along the elevational gradient so that each taxon was equally weighted. We used two indices, one based on predator abundance and the other based on predator species richness.

Data analysis

Geometrid samples were characterised by the number of individuals and species, standardised per sample size. The abundance was expressed per seven sampling nights, and the number of species per 355 individuals at each site, obtained by rarefaction. These were the smallest sample sizes available per elevation. Species richness was analysed using individual-based species accumulation curves extrapolated and interpolated to comparable sample sizes at different elevations (Chao et al., 2014). Total species richness was estimated using the Chao 1 nonparametric estimator based on the abundance of rare species in the samples (Gotelli & Colwell, 2001).

Beta-diversity among communities was quantified using the Sorensen index and partitioned into species turnover (Simpson dissimilarity) and nestedness (Sorensen–Simpson dissimilarity) (Baselga & Leprieur, 2015). We also used Bray–Curtis similarity, which is a quantitative version of the Sorensen index, as a measure dependent on abundance rather than species presence/absence. We used EstimateS 9.1.0 software to calculate all diversity indices (Colwell, 2013).

The elevational distribution of the species sampled as ≥10 individuals was characterised by the elevation range, defined as the difference between maximum and minimum recorded elevation. The mean elevation range was then estimated for each geometrid community, based on the presence/absence of species as well as weighted by their abundance.

We used key variables characterising the abiotic environment (mean annual temperature), food resources (basal area and species richness of vegetation) and natural enemies (the indices of predator abundance and species richness) in a GLM model to examine potential factors influencing abundance and species richness of geometrids along elevational gradients. In addition, we examined the effects of temperature, predator abundance and species composition of the vegetation on species composition of geometrids using canonical correspondence analysis (CCA) ordination implemented in CANOCO 5.04 software. The plant species composition for each elevation was characterised by its first axis score obtained by DCA ordination of log-transformed basal area data from the plant plots.

RESULTS

Species richness and abundance

We recorded a total of 16,424 geometrid individuals collected in 76 sampling nights at eight sites along the Mt. Wilhelm elevation gradient. The careful analysis of external morphology revealed 978 morphospecies. Subsequent successful COI sequencing of 1582 specimens, selected to represent as many species-elevation combinations as possible, resulted in the synonymisation of 31 originally detected morphospecies and the recognition of an additional 155 previously unrecognised species, bringing the total to the current 1102 species.

The species accumulation curve for the entire transect converged with the Chao1 estimate of a total of 1166 species (Figure 1a). Randomised species accumulation curves for individual surveys approached the asymptote and their relative diversity ranking was generally independent of sample size, including diversity extrapolated to 2500 individuals (Figure 1b). Species diversity correlated with
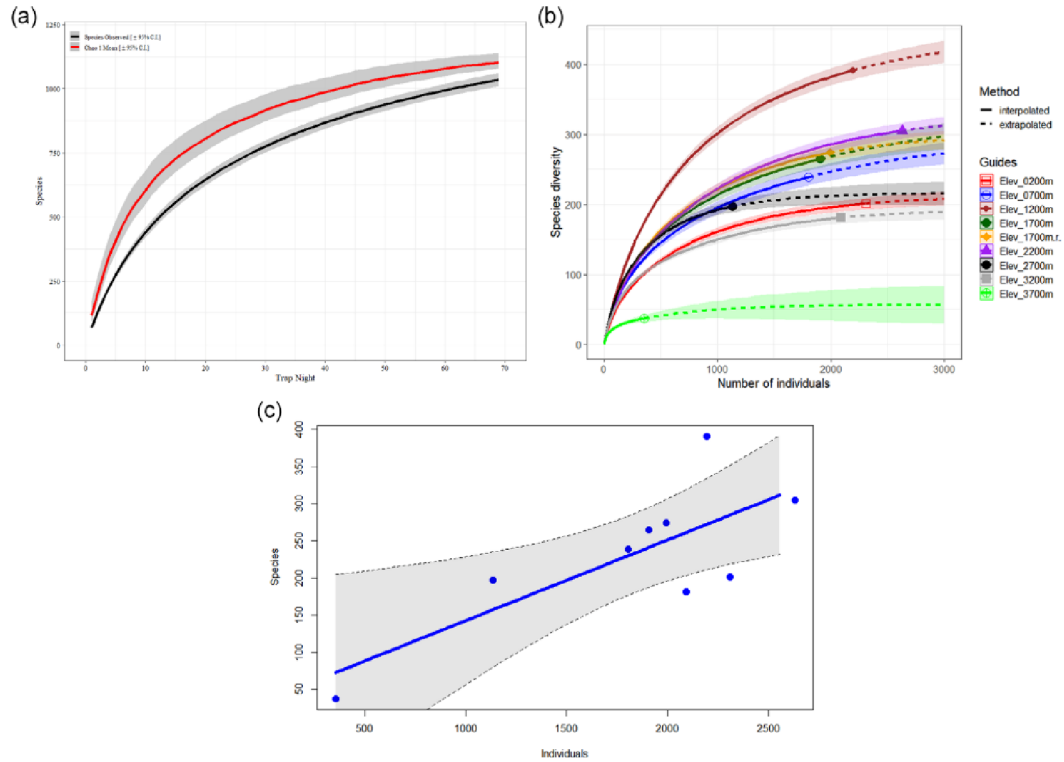

FIGURE 1 Randomised species accumulation curve and the Chao1 total species richness estimate (with 95% CI) for the entire elevational transect (a), the species accumulation curves for individual elevations (b), and the correlation between moth abundance and species richness per site along the elevational transect (Pearson $r = 0.76$, $p < 0.001$, $N = 8$) (c).
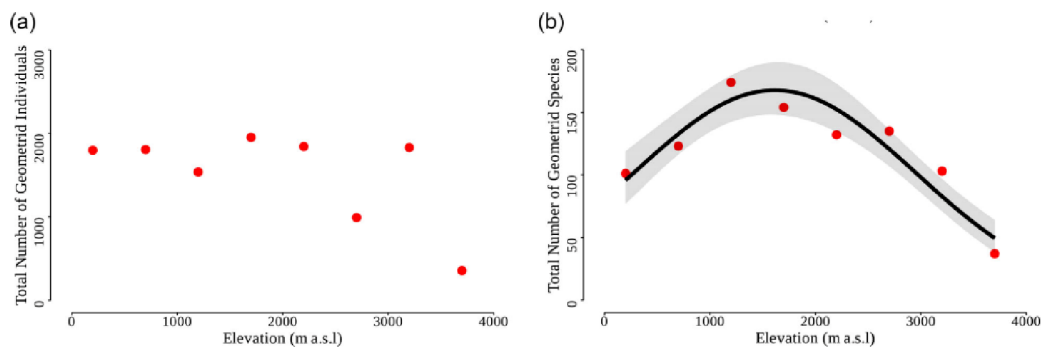

FIGURE 2 The elevational trends in geometrid abundance per seven sampling nights (a) and species richness per 355 individuals (b). The correlation with elevation is not significant for abundance, while the number of geometrid species is best fitted by a second order polynomial with Poisson distribution (Species = Elevation + I(Elevation2) + season) ($p < 0.01$).

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abundance across elevations (Figure 1c). There was no significant trend in geometrid abundance as a function of elevation, while the number of species standardised per 355 individuals peaked at mid-elevation at approximately 1200 m asl (Figure 2). The maximum diversity at mid-elevation was observed in both dry and wet season samples (Figure S2).

The relative importance of individual subfamilies, both in terms of the number of species and individuals, changed with elevation (Figure S3). The share of Sterrhinae and Geometrinae decreased and that of Larentiinae increased with increasing elevation, while the most abundant subfamily Ennominae exhibited a mid-elevation maximum for the number of individuals and a constant share of species diversity across elevations.

Similarity between geometrid communities decreased with the logarithm of their elevation distance, with all pairs of communities separated by >1000 m elevation having Bray Curtis similarity <0.15 (Figure S4). The main driver of beta diversity is species turnover, which on average accounts for 92% of total beta diversity across all pairwise comparisons between elevation sites.

Beta diversity over 500 m elevation between sample pairs from adjacent sites increased with increasing elevation (Figure 3). It was also dominated by species turnover, which accounted for 65%–99% of total beta diversity; nestedness accounted for 55% of beta diversity only between 3200 and 3700 m elevations. This suggests that the geometrid community at the timberline is a subset of a more diverse community from lower elevations.

The decreasing similarity of communities with elevation is a consequence of the parallel trend of decreasing mean elevational range of species in the geometrid communities. When mean elevational range is weighted by species abundance, it decreases from 1264 m at 200 m asl. to 633 m at 3700 m asl. This trend also holds for the mean elevational range based on the presence/absence of species (Figure 4).

Elevation trends in basal area and number of species for woody plants, which represent a potential resource base for herbivorous geometrids, show an approximately unimodal response to elevation, but with maxima at different elevations: at 1200 m asl. for species and at 2700 m asl. for basal area (Figure 5). Thus, there is broad agreement between trends in plant and geometrid species richness, but not between plant basal area and geometrid abundance. Predation pressure, measured as the abundance and species diversity of insectivorous birds, bats and ants shows a largely monotonic decrease with increasing elevation (Figure 5).

Geometrid abundance was not significantly correlated with elevation and could not be explained by any combination of mean annual temperature, predator abundance and plant basal area (Table S1). Geometrid species richness was best explained by plant species richness (Table S1). Geometrid community species composition was partially explained by temperature, predator abundance and plant species composition. The three significant variables accounted for 38.7% of the total variability in species composition ($F = 1.4$, $p < 0.05$, Monte Carlo test) (Figure 6).
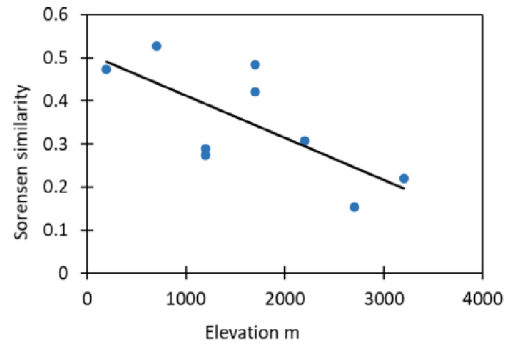

FIGURE 3   Sorensen similarity between pairs of adjacent sites separated by 500 m elevation difference (Pearson $r = -0.71$, $p = 0.031$). The elevation of the lower site is used for each similarity value.
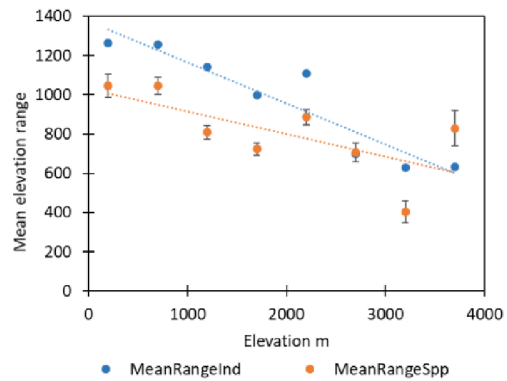

FIGURE 4   The relationship between mean elevational range for individuals (Pearson $r = -0.94$, $p < 0.05$) and species (Pearson $r = -0.68$, $p < 0.05$, based on species sampled as ≥10 individuals) and elevation.

DISCUSSION

Our Mt. Wilhelm dataset recorded one of the highest geometrid diversities along a rainforest elevation gradient (Beck et al., 2017), surpassed only by elevational gradients in the Andes (Beck et al., 2017; Brehm et al., 2005; Holloway et al., 2009). The diversity of herbivorous Geometridae may depend in part on vascular plant diversity, which reaches one of six global maxima in the Mt. Wilhelm area (Kier et al., 2005), although the plant-geometrid correlation may be weakened by an increasing role of 'alternative feeders', specialising on epiphylls, lichens, and dead leaves in montane forests (Bodner et al., 2015).

Results of this study demonstrate the importance of molecular data for species definition, because even after careful morphotyping,
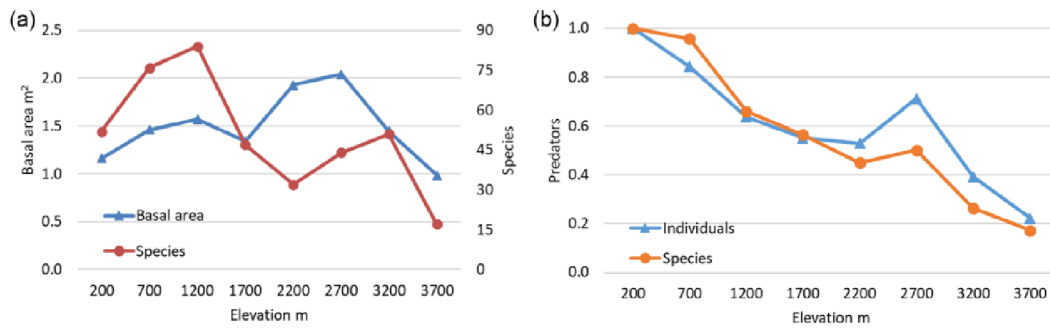
FIGURE 5 (a) Elevational trends in basal area (in m^2) and number of species per 1200 m^2 for woody plants with DBH ≥5 cm. (b) Elevation trends in the relative number of predatory species and individuals, calculated as mean values for insectivorous birds, insectivorous bats and ants standardised to the (0, 1) range.
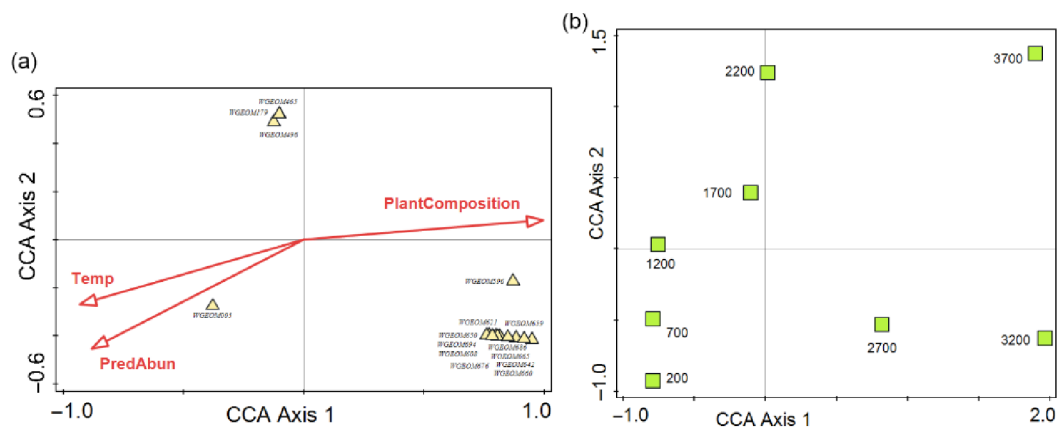

FIGURE 6 CCA ordination of geometrid species (L) and communities from different elevations (R) with the temperature, plant composition and predator abundance as explanatory variables. All variables are significant (Monte Carlo test, $p < 0.05$) and together explain 38.69% of the variation in community composition. Only the 20 most common species shown.

subsequent information on COI sequences changed the species definition of 19% of the original 987 morphospecies by either synonymizing or subdividing them. However, this is still significantly less than the 80% increase reported from a neotropical elevational gradient (Brehm et al., 2016).

On the Mt. Wilhelm transect, butterfly and bird diversity decreased with increasing elevation, while ants and ferns exhibited a peak at mid-elevation (Colwell et al., 2016). A peak in species richness at mid-elevation, between 600 and 1700 m asl. in the tropics, is the most common pattern for geometrids (Beck & Chey, 2008; Beck et al., 2017; Brehm et al., 2005; but see Brehm, Süssenbach, & Fiedler, 2003). This is a robust pattern that is not influenced by anthropogenic disturbance, geographic region, or climate (Beck et al., 2017). The diversity peak may shift within a few hundred metres of elevation depending on seasonality (Beck et al., 2010; Maicher et al., 2019), but this was likely not the case in our study system.

The species richness trends in geometrids are composite patterns combining individual subfamilies (Brehm & Fiedler, 2004). The subfamilies Ennominae, Geometrinae and Sterrhinae, with larger body sizes, dominate at mid-elevations, while the small-bodied Larentiinae dominates at higher elevations, potentially because there are many lichen feeders in this subfamily (Beck & Chey, 2008; Brehm & Fiedler, 2003, 2004; Brehm, Homeier, & Fiedler, 2003; Brehm, Süssenbach, & Fiedler, 2003). Similar composite trends in diversity are also evident in other megadiverse moth families such as Arctiidae, Pyraloidea and Sphingidae (Bärtschi et al., 2019; Fiedler et al., 2008).

A global analysis by Beck et al. (2017) showed that there is no obvious single variable explaining the nearly universal mid-elevation maximum in geometrid diversity. Even multivariate models, when successful, provided idiosyncratic explanations for some of the data sets, with some support for variables such as primary productivity and land

area, temperature, and the mid-domain effect (Beck et al., 2017; Evans et al., 2005; Maicher et al., 2019; McCain, 2007). Multi-taxa analyses of other moth families have found that temperature is an important driver of diversity (Bärtschi et al., 2019; McCain, 2007, 2009; Peters et al., 2016). In addition, primary productivity is important because it determines the diversity of food resources (Evans & Gaston, 2005).

The relationship between plant and geometrid diversity is complicated by the variable host specificity of geometrid species and the fact that many plant lineages do not host geometrid herbivores (Holloway, 1993, 1996, 1997; Novotny et al., 2002). While some studies found no correlation between plant richness or basal area and geometrid species diversity (Axmacher, Holtmann, et al., 2004; Axmacher, Tünte, et al., 2004; Axmacher et al., 2009), plant species richness at Mt. Wilhelm was the best explanatory variable for geometrid species richness, while plant composition partly explained species composition of geometrids.

A mid-elevation maximum may also result from a combination of monotonic factors acting in opposite directions, such as decreasing energy density and area size versus decreasing predation pressure with increasing elevation. Predation pressure measured more directly as attack rates on dummy caterpillars decreased with elevation at Mt. Wilhelm (Sam et al., 2015) and globally (Roslin et al., 2017). Beck and Chey (2008) tested five variables using segmented regression, thus drawing different sets of explanatory variables for the upward and downward trends in species richness along the transect. This is a promising approach, but their analyses lacked data on predation, while our data are limited to only eight elevations.

As expected, community similarity decreased as a logarithmic function of elevation distance among study sites (Brehm, Homeier, & Fiedler, 2003). The rapid species turnover contrasts with low beta diversity over distances within the lowland rainforests of New Guinea (Novotny et al., 2007). The mean elevational range of geometrid species decreased with elevation, a pattern contrary to that expected under Rapoport's rule (Stevens, 1992). Rapoport's rule suggests that high temperature variability leads to greater temperature tolerance in high-elevation species and thus their greater elevational ranges. Beck et al. (2016) confirmed this relationship between temperature variability and geographic range size for geometrids but noted that temperature variability does not necessarily increase with elevation in the tropics.

The increasing species turnover across 500 m elevation with increasing elevation refutes the hypothesis that the peak in alpha diversity at mid-elevation is caused by mixing of two different species groups—lowland and montane, as this would lead to a peak in beta diversity at mid-elevation (Beck & Chey, 2008). Beta diversity has generally been determined by species change rather than nestedness. This is expected for successive replacement of individual lineages, such as subfamilies, with elevation.

The total of 1102 species found along the transect represents 280% of the highest local diversity recorded at 1200 m asl. This is the third highest transect-to-community ratio among taxa surveyed along the Mt. Wilhelm gradient (Novotny & Toko, 2015), highlighting the key role of elevational gradients in maintaining high regional diversity.

This species enrichment makes long elevation gradients in the tropics priority areas for biodiversity conservation. Mt. Wilhelm National Park includes only 800 ha of alpine ecosystems, representing a small minority of all species along the entire gradient. Based on recent biodiversity surveys, including this study, an expanded protected area is proposed (Novotny & Toko, 2015). Protecting continuous, long elevation gradients is increasingly important because they allow species to redistribute in response to climate change.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The author declares that there is no conflict of interest for any author.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

Table S1. Generalized linear models (GLMs) testing the effects of temperature, plants species richness and predator species richness on geometrid species richness, and the of temperature, plant basal area and predator abundance on geometrid abundance. The best model is in bold.

Figure S1. Mt. Wilhelm elevation transect comprising eight study sites separated by 500 m elevational intervals. Inset: Papua New Guinea with the Mt. Wilhelm study area. Map from Moses et al. (2021).

Figure S2. Elevation trends for species richness per sampling night for the wet (blue) and dry (red) seasons. The GLM model using log-link and Poisson distribution (Species = Elevation + I(Elevation2) + season) ($p < 0.01$).

Figure S3. The dominance of geometrid subfamilies in terms of number of individuals (a) and species (b) along the Mt. Wilhelm elevation gradient.

Figure S4. The relationships between Bray–Curtis similarity of geometrid communities and the difference in their elevation.

Supplementary Information

Table S1: Generalized linear models (GLMs) testing the effects of temperature, plants species richness and predator species richness on geometrid species richness, and the of temperature, plant basal area and predator abundance on geometrid abundance. The best model is in bold.

Dependent var.	Model	log(L)	Akaike w.	AICc	deltaAICc
Species richness	Null	-41.694	0.215	89.789	2.377
	Plant species + Temperature + Predator species richness	-35.837	0.000	111.673	24.262
	Plant species + Predator species richness	-37.647	0.007	96.627	9.216
	Plant species + Temperature	-37.671	0.007	96.676	9.264
	Temperature + Predator species richness	-40.167	0.001	101.668	14.257
	Plant species	**-37.706**	**0.707**	**87.411**	**0.000**
	Temperature	-40.606	0.039	93.211	5.800
	Predator species richness	-41.083	0.024	94.166	6.754
Abundance	**Null**	**-63.095**	**0.717**	**132.589**	**0.000**
	Plant basal area + Temperature + Predator abundance	-60.494	0.000	160.987	28.398
	Plant basal area + Predator abundance	-61.914	0.001	145.162	12.572
	Plant basal area + Temperature	-60.497	0.006	142.327	9.738
	Temperature + Predator abundance	-61.860	0.001	145.053	12.463
	Plant basal area	-63.061	0.045	138.122	5.532
	Temperature	-61.909	0.143	135.818	3.229
	Predator abundance	-62.410	0.087	136.819	4.230

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Figure S1. Mt. Wilhelm elevation transect comprising eight study sites separated by 500 m elevational intervals. Inset: Papua New Guinea with the Mt. Wilhelm study area. Map from Moses et al. (2021).

Figure S2. Elevation trends for species richness per sampling night for the wet (blue) and dry (red) seasons. The GLM model using log-link and Poisson distribution: Species = Elevation + I (Elevation^2) + season) (P<0.01).

Figure S3. The dominance of geometrid subfamilies in terms of number of individuals (**A**) and species (**B**) along the Mt. Wilhelm elevation gradient.

$$y = -0.054\ln(x) + 0.4671$$
$$R^2 = 0.408$$

Figure S4. The relationships between Bray-Curtis similarity of geometrid communities and the difference in their altitude.

CHAPTER II

Composition and structure of rainforest moth (Geometridae, Lepidoptera) communities along an island elevational gradient in New Britain (Papua New Guinea)

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(Manuscript)

Composition and structure of rainforest moth (Geometridae, Lepidoptera) communities along an island elevational gradient in New Britain (Papua New Guinea)

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Keywords: altitudinal gradient, species diversity, beta diversity, insect herbivory, geometrids, tropics, Melanesia

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Running title: Rainforest moths along an island elevational gradient

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Abstract

1. Rainforest elevational gradients on islands of different sizes represent an interesting system combining the effects of island biogeography and biotic and abiotic gradients on species diversity. We studied geometrid moths along a rainforest gradient extending from 500 to 1100 m asl. in the Whiteman Range on New Britain Island and compared it to a nearby elevational gradient on Mt Wilhelm on the much larger island of New Guinea.

2. The 16,687 individuals collected with light traps at four elevations represented 362 species. This comprised an estimated 86% of the total number of species, providing a representative sample of a species-rich insect community.

3. Species diversity of geometrid communities on the Whiteman Range was similar to that on Mt. Wilhelm. The effect of island size on species diversity was not detected.

4. Species composition of geometrids along the Whiteman Range was partially explained by parallel gradients in mean annual temperature and plant species composition.

5. There was a large overlap in species composition between Whiteman Range and Mt. Wilhelm, and population sizes of the species shared between both transects were correlated. This suggests possible dispersal between the two montane ranges on both short and long time scales.

6. The total of 1,317 species documented for the two montane ranges indicates an exceptionally diverse geometrid fauna in the New Guinea region, probably even more diverse than that of Borneo.

7. Data on model insect communities such as geometrids are important for future monitoring of potential climate change impacts and insect decline trends.

Introduction

Altitudinal gradients of rainforests in the humid tropics tend to combine high local alpha diversity of insect communities with rapid turnover of species with increasing elevation along a wide range of elevations, from lowlands to the timberline at 3600–4000 m asl. (Erwin 1982, Stork 1988, Novotny et al. 2002, Beck et al. 2017, Toko et al. 2023). Rainforest elevation gradients are therefore among the world's most important biodiversity hotspots (Beck et al. 2017, Rahbek et al. 2019). At the same time, the number of complete rainforest gradients with undisturbed rainforests spanning the entire climatically suitable altitudinal range is limited, especially in the Paleotropics (Rehm & Feeley, 2015). Given growing concerns about the impacts of climate change on biodiversity, elevational gradients are also increasingly important natural "laboratories" for ecologists to study community dynamics and ecological factors that determine species distributions in different climates. In particular, mean annual temperature decreases linearly with elevation, at a rate of 5.4 °C per 1000 meters of elevation in PNG (Sam et al. 2019).

There are two common patterns of species distribution along elevational gradients: (1) the monotonic decrease in species diversity with increasing elevation and (2) the unimodal pattern with the highest number of species at intermediate elevations (Rahbek 1995, McCain 2005, 2007, 2009, 2010, Colwell et al. 2016, Peters et al. 2016, Beck et al. 2017). Numerous hypotheses have been proposed to explain the mechanisms driving these patterns, including abiotic factors (temperature and precipitation), geographic factors (area size and mid-domain effect), and biotic factors (resource abundance and predation pressure), but no consensus has been reached on taxa and geographic locations (McCain 2007, Colwell et al. 2016, Beck et al. 2017). Our analysis of a complete rainforest elevational gradient at Mt. Wilhelm in the Central Range has pointed to the potential importance of plant diversity, temperature, and predation pressure in determining a peak in mid-elevation geometrid diversity documented there (Toko et al. 2023).

The Geometridae (Lepidoptera) are one of the three most species-rich moth families, with over 24,000 described species (Rajaei et al. 2022). They lend themselves to community studies and are therefore often studied as a model taxon because Geometridae [i] adults can be efficiently sampled with light traps, [ii] local species diversity is high but manageable, [iii] species are distributed over a wide range of altitudinal ranges, [iv] species range from specialists to generalists, and [v] species-level taxonomy is more advanced than in many other moth families (Rajaei et al. 2022). Herbivorous caterpillars are sensitive to vegetation changes, making them a suitable taxon for studying vegetation dynamics and succession (Holloway et al. 1992, Kitching et al. 2000, Chen et al. 2009, Ashton et al. 2016).

The present study focuses on New Guinea that is exceptional in comprising several high-montane ranges characterized by different ages, geologic histories, and geographies (Toussaint et al. 2014). In particular, the Central Range in New Guinea, which is 10 million years old, contrasts with oceanic island arcs that gradually dock onto the northern coast of New Guinea coast, uplifting separate younger mountain ranges (Bewani-Toricelli Mts., Finisterre-Saruwaged Mts., Adalbert Mts.), as well as montane ranges still isolated on nearby islands, including the Whiteman Range in New Britain, which will dock with mainland New Guinea in the future (Touissant et al. 2014).

While New Guinea is a large island whose evolutionary dynamics and ecological diversity resemble a small continent (Gressitt 1982, Heads 2002, Cámara-Leret et al. 2020), New Britain is the largest among the oceanic islands of the Bismarck Archipelago, accounting for 8% of the area of mainland New Guinea. It is separated from the mainland of New Guinea by the Vitiaz Strait 1,200 m deep but only 100 km wide. This geographic location allows us to test hypotheses about differences between elevational trends in insect communities on large and small islands, as well as hypotheses about isolation and endemism of island insect faunas. In particular, we expect lower species diversity in New Britain communities that were never historically connected with the island of New Guinea, and

high species turnover between corresponding elevations in the Central Range and New Britain.

Material and Methods

Study area

We selected four study sites separated by 200 m elevation difference, from the lowest available undisturbed primary forests at 500 m asl. through 700 m and 900 m asl. to the mountain top at 1100 m asl. along an elevation gradient on the slopes of the Whiteman Range in the West New Britain (Figure S1, Table S1). Forests below 500 m asl. were mostly secondary, partially logged, and partially converted to oil palm plantations by smallholders. We found that much of the lowland rainforest between 200 and 500 m asl. in a wider area was either selectively but heavily logged or converted to a mosaic of small to large oil palm plots. Most of the forests remaining after these disturbances and land conversions consisted of fast-growing, late-successional forests, which were not studied here. Mean annual temperature ranged from 19.4 to 27.0°Celsius along the elevation gradient, with mean annual precipitation of about 3950 mm (Harris et al. 2020).

The Whiteman Range runs from the western end of the island of New Britain and joins the Nakanai Range at the eastern end, forming the central cordillera of the island of New Britain. It is a tectonically active area with some of the longest caves in the world, deep volcanic craters, and fast-flowing surface and submerged rivers that contribute to frequent natural forest disturbances. Data from the Whiteman Range were compared with a 200–3700 m asl. rainforest transect at Mt. Wilhelm in the Central Range of New Guinea Island, described in detail in Toko et al. (2023).

Geometrid sampling and identification

We conducted two field surveys (October - December 2015 and October - November 2017) at each of the four study sites. We collected geometrid

moths from primary forests using standardized sampling of nine trapping nights per survey and site, for a total of 72 sampling nights. We used manual sampling on a 1 x 2 m white sheet illuminated by a 250 W mercury vapor bulb (Fig. S2). We sampled from 18.00 to 24.00 every night. As far as possible, we mounted 10 voucher specimens per species, which were deposited at the New Guinea Binatang Research Center, PNG, and the National Museum of Natural History, Smithsonian Institution, USA. Species identification was based on morphology using the book The Moths of Borneo (Holloway 1993, 1996, 1997) and a reference collection from our parallel elevation survey at Mt Wilhelm on the main island of New Guinea, which was also supported by extensive COI barcoding (PAGIB in Barcode of Life, (Toko et al. 2023)). The morphospecies from the Whiteman Range and Mt. Wilhelm were cross-referenced, allowing the comparison of species composition between the communities from both montane ranges. The collections were deposited at the New Guinea Binatang Research Center.

Data Analysis

Geometridae community samples were standardised based on sampling duration, i.e., 18 trapping nights per site, combining both surveys. The effect of sampling duration on total species richness along the transect was examined using randomised species accumulation curves along with the Chao 1 total species richness estimator. Species diversity per elevation was analysed using individuals-based extrapolated and interpolated rarefaction curves (Chao et al. 2014). We have also standardised species richness for 355 individuals, the smallest sample size per elevation for the combined data set from Whiteman Range and Mt. Wilhelm.

We calculated beta diversity using Bray-Curtis dissimilarity, which depends on species abundance and is most strongly influenced by common species, and Sorensen similarity using species incidence data, so that all species were weighted equally regardless of abundance. Since tropical samples with large numbers of rare species are sensitive to sampling bias, we have also used the Chao-Sorensen correction of the similarity index for

missing species. We used the EstimateS 9.1.0 programme to calculate our alpha and beta diversity parameters (Colwell 2013). Beta diversity was calculated for all sample pairs, both within and between the two elevational gradients. Beta-diversity among communities also partitioned into species turnover (Simpson dissimilarity) and nestedness (Sorensen–Simpson dissimilarity) based on Baselga & Leprieur (2015).

Canonical correspondence analysis (CCA) was used to examine the influence of temperature and vegetation composition on geometrid community composition. Vegetation composition data were obtained from a survey of three 20x20 m plant plots per elevation, in which all plants with a DBH≥5cm were measured, recorded, and identified to (morpho)species. Plant data were then analysed using a DCA ordination, using log-transformed basal area data. The first axis coordinates were used as the plant composition index for the geometrid species composition analysis. We used CANOCO 5.04 software for all ordinations (Šmilauer and Lepš 2014).

Results

We collected 362 species and 16,687 individuals on 72 trap nights along the Whiteman Range elevation gradient. The total number of species observed and estimated increased with increasing sample size, but approached the asymptote for both the entire transect (Fig. 1a) and individual elevations (Fig. 1b), indicating that we were able to capture a majority of the species present. The Chao-1 estimate for the entire transect was 419 species with a 95% confidence interval of 390 to 475 species (Fig. 1a).

Local species diversity at each elevation ranged from 197 species at 500 m asl., 216 species at 700 m asl., 229 species at 900 m asl., and 247 species at 1100 m asl., indicating no clear elevational trend. This is also evident from the overlapping confidence intervals for the species accumulation curves for each elevation (Fig. 1b). Species richness extrapolated to 8,000

individuals also showed a narrow range from 200 to 260 species with no significant differences among elevations (Fig. 1b). The common trajectory of the species accumulation curves indicates that the differences in species richness among elevations are primarily due to differences in abundance. Abundance of geometrids per the 18 sampling nights increased from low values of 2590 and 2874 individuals at 500 m and 700 m elevation, respectively, to 4829 individuals at 900 m asl. and the peak value of 6394 individuals at 1100 m asl. (Fig. 1b).

Species richness was also standardized to 355 individuals for comparison with the Mt. Wilhelm transect, where this was the smallest sample obtained for the 3700 m asl. elevation (Fig. 2). The species diversity at the Whiteman Range sites ranged from 92 to 116 species per elevation, comparable to the diversity at Mt Wilhelm at the corresponding elevations.

Beta diversity between adjacent sites separated by 200 meters of elevation was low at 70% of species shared between sites and showed no elevation trend (Fig. 3a). This is also reflected in the approximately balanced number of species occurring at each of the lower and upper elevations compared (Fig. 4). On average, 88% of species change between elevations was due to species turnover and 12% due to nestedness. The dissimilarity between communities based on the abundance and composition of species, measured by Bray Curtis dissimilarity index, increased with increasing elevational distance between pairs of samples (Fig. 3b).

The similarity decay with increasing elevation difference between the compared geometrid communities was examined using the Sorensen and Chao-Sorensen indices, for each of the two transects separately and also for mixed pairs of communities, each from a different transect (Fig. 5). For a given elevation difference, the rate of species turnover is lowest in the Whiteman area, followed by Mt. Wilhelm, and finally by mixed samples from both transects.

Both transects were sampled at similar elevations in the range of 400 – 1200 m asl. For geometrid species present on both transects, there was a

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weak but significant correlation between their abundance on the Whiteman and Mt Wilhelm transects (Fig. 6).

The basal area and species richness of woody plant communities increased with increasing elevation (Fig. 7). Plant species composition, quantified as DCA1 axis from their ordination based on basal area, aligns well with temperature in the ordination of geometrid communities (Fig. 8), suggesting an important influence of elevation. Plant composition and temperature together explain 25% of the variability in geometrid communities.

Figures
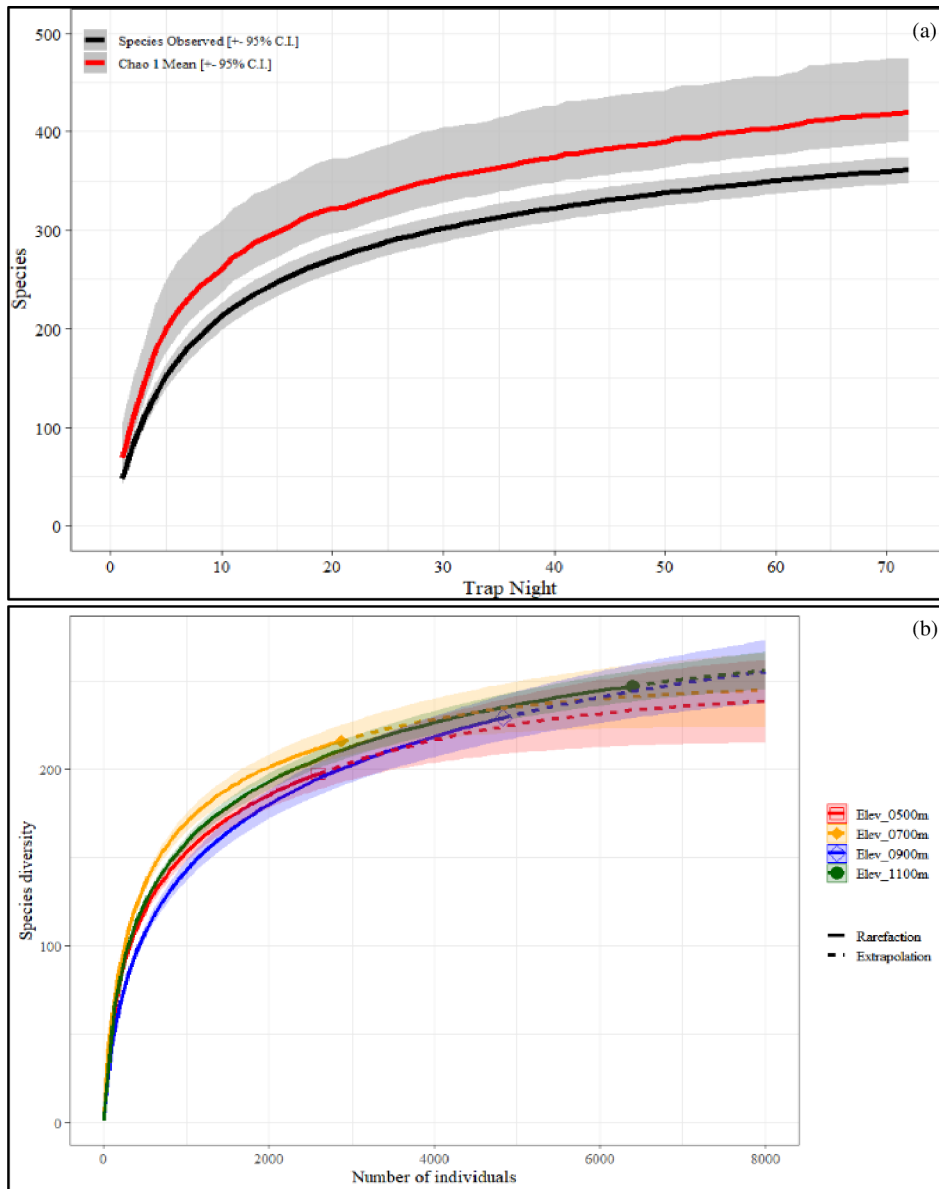
Figure 1. (a) The randomized sample-based species accumulation curve for the entire Whiteman Range transect, showing observed number of species (black line) and the total number of species estimated by Chao1 index (red line), with 95% confidence intervals. **(b)** Randomized individual-based species accumulation curves (with 95% confidence intervals) for individual elevations, extrapolated (dashed lines) to the sample size of 8,000 individuals per elevation.
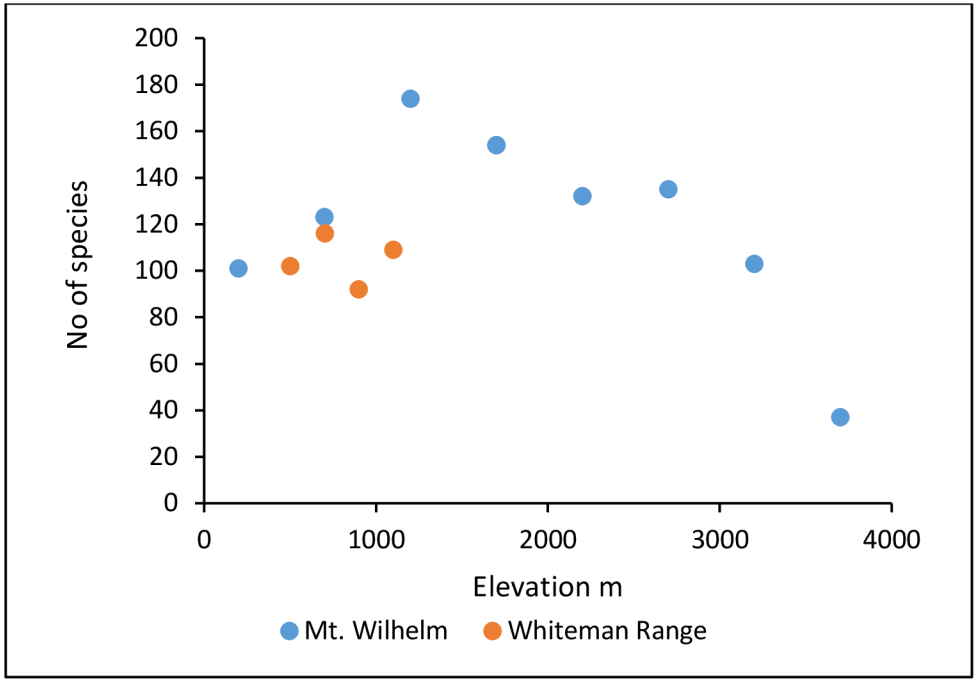
Figure 2. The number of species standardised by rarefaction per 355 individuals for the Whiteman Range and Mt Wilhelm, showing comparable species diversities between the two transects.
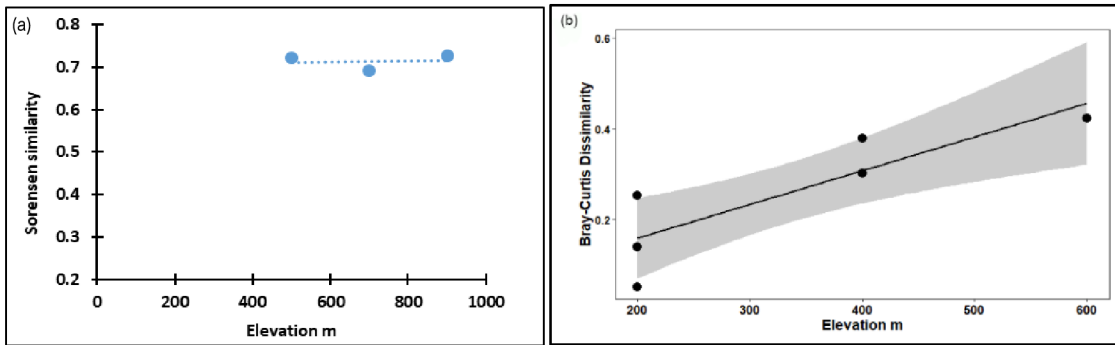
Figure 3. (a) Sorensen similarity between pairs of adjacent sites, separated by 200 m elevational difference (Pearson r = 0.13, p = 0.92), **(b)** Bray-Curtis dissimilarity for all pair-wise site comparisons, increasing with increasing elevation difference (r = 0.92, p < 0.05, Mantel test, 999 runs).
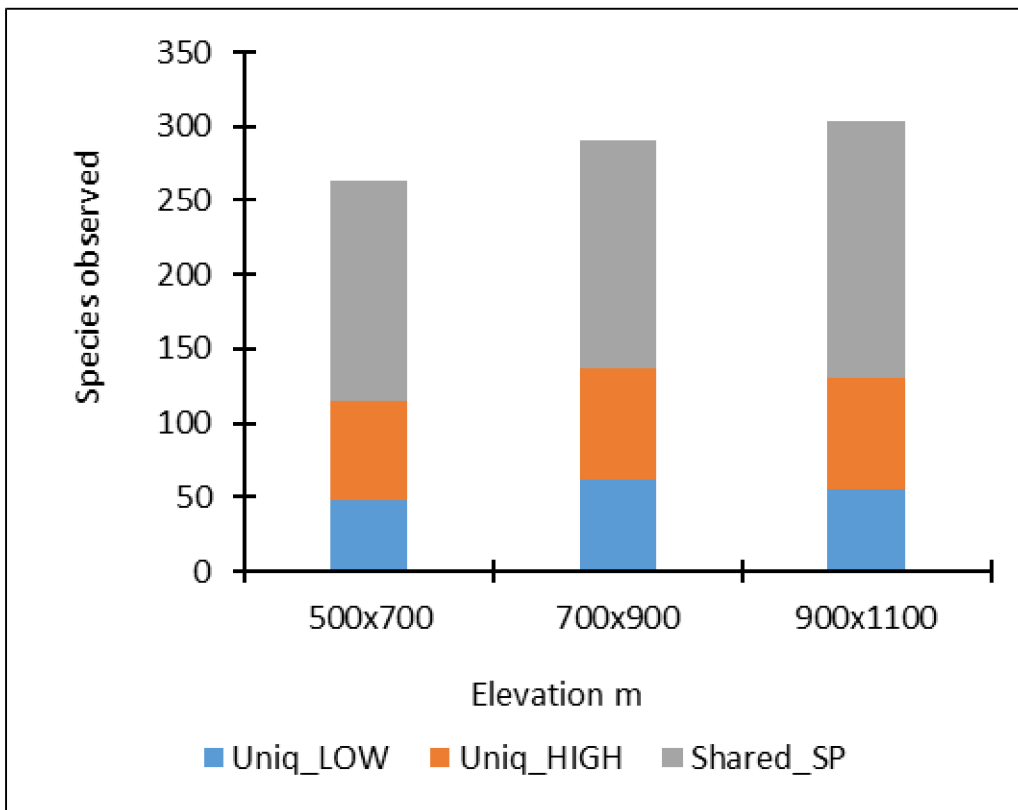
Figure 4. The number of shared species and the species unique for the lower and the higher elevation between pairs of adjacent elevations in the Whiteman Range

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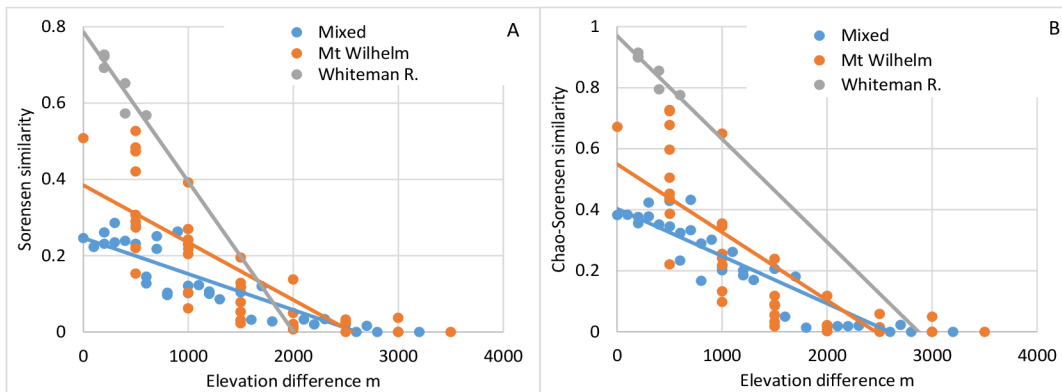
Figure 5. The Sorensen **(A)** and Bray Curtis **(B)** similarity between pairs of geometrid communities separated by various elevation differences within the Whiteman Range transect (grey markers and line), Mt Wilhelm transect (orange) and between the transects (blue).
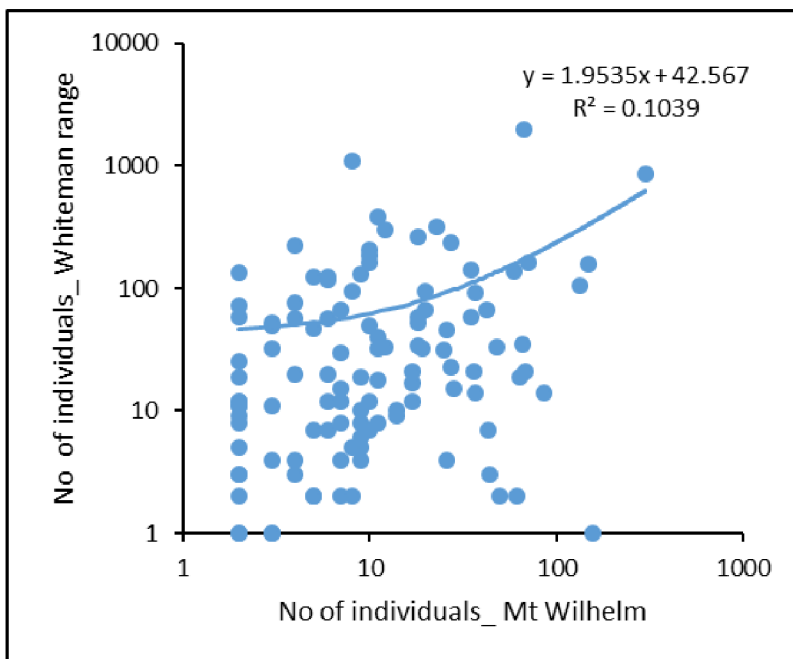
Figure 6. The relationships between the number of individuals in the Mt Wilhelm and Whiteman range transects sampled below 1200 m asl. for the geometrid species shared between the two transects. There is a positive correlation between the two abundances, explaining 10% of variability in abundance.

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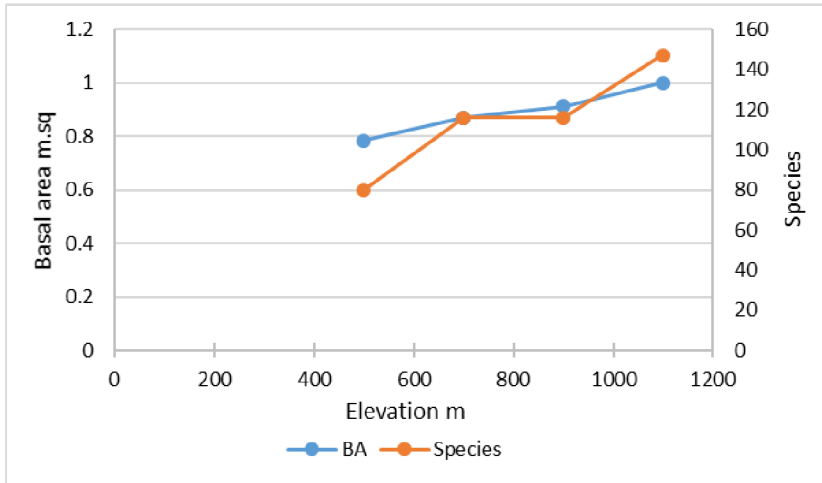
Figure 7. The elevational trend for the number of species and basal area (BA) for woody plant species with DBH ≥ 5cm per 1200 m^2 area.
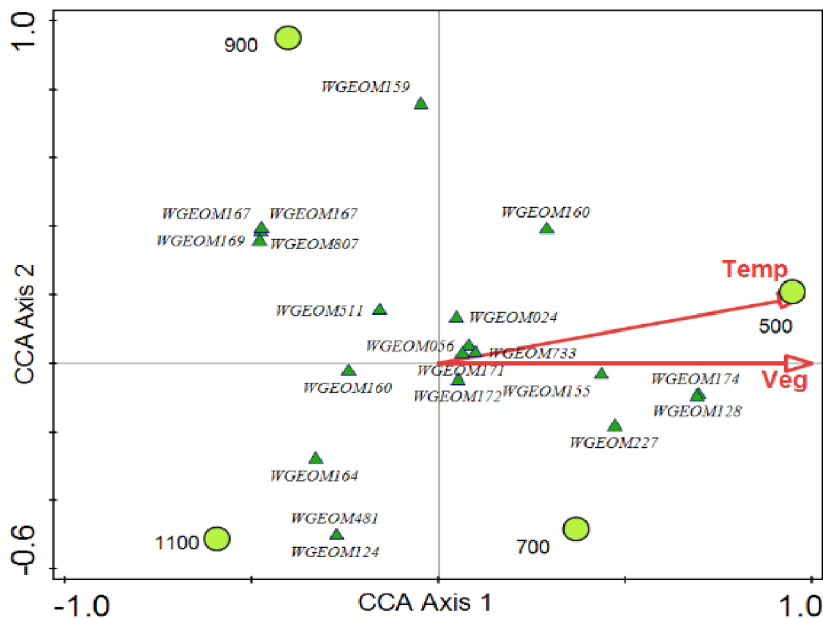
Figure 8. Species composition of geometrid communities explained by temperature and vegetation in a CCA ordination. Both variables are aligned with 1st axis, significant (F = 2.0, P = 0.046, Monte Carlo test of the 1st axis), adjusted explained variation 25.25%. Only 20 most common species are shown in the diagram.

Discussion

Our study in the Whiteman Range provided one of the first quantitative community samples for geometrids from the Bismarck Archipelago, an area of high species diversity and endemism (Heads 2002). Based on asymptotic Chao1 estimate, we determined about 86% of the total species present, which is a high proportion for tropical insect samples. These results may establish a standard of about 15 trap nights per site as sufficient to capture most of the species diversity of Geometridae in a tropical rainforest community, as an example of a model taxon with high diversity of herbivorous insects in tropical forests (Beck et al. 2017).

The limited elevation range available for the primary rainforest in New Britain, between 500 and 1100 m asl., has meant that strong elevation trends are not evident in the communities studied. While the upper limit of the elevation range was defined by geography, it is notable that nearly half of the geographically possible elevation range of the rainforest, from 0 to 500 m asl., was not available due to disturbance. Thus, we were able to study only 600 metres of elevation out of the theoretically available 3700 metres between the ocean coast and the tree line in the New Guinea region, as shown in our other study at Mount Wilhelm.

Interestingly, the overlapping elevations of the Whiteman Range and Mt Wilhelm studies, between 500 and 1100 m asl., had comparable geometrid diversity. Given the considerably smaller area of the entire island of New Britain and the central montane range, we had expected lower diversity than on the main island of New Guinea. However, it is possible that dispersal between the two transects could offset the areal effects on species diversity.

As expected, the similarity of geometrid communities from different montane ranges was lower than within a single region. However, the mean Chao-Sorensen estimate of 39% species overlap between two sites 500 m apart, one from the Whiteman Range and another from Mt Wilhelm, was relatively high compared to the mean overlap of 53% for nine such

comparisons available within the Mt Wilhelm transect. Interestingly, the abundances of shared species are correlated between the two ranges, although the correlation explains only 10% of the community variability. This correlation could be a result of dispersal or parallel patterns in host plant composition between the two ranges. The overall diversity of geometrids in the Whiteman Range was limited by low overall elevation. The lack of higher elevations in New Britain likely greatly reduced the regional species pool, judging from the parallel patterns at Mount Wilhelm, where geometrid species diversity peaked at 1200 m asl. (Toko et al. 2023).

The Whiteman Range geometrid communities showed an increase in abundance with increasing elevation, unlike at Mt. Wilhelm where there was no elevation trend in abundance (Toko et al. 2023). However, there were no clear patterns in alpha or beta species diversity over the limited elevational range of the transect. This is consistent with a generally high overlap in species composition between adjacent sites 200 metres in elevation apart. It appears that this difference in elevation, corresponding to a difference of about 1°C in mean annual temperature, is not a significant constraint on the dispersal of species or the distribution of their host plants. Beta diversity of geometrids was mainly determined by species turnover rather than nestedness, consistent with other tropical communities dominated by a large number of rare species (Toko et al. 2023).

The limited elevational range of the transect also does not allow for detailed analysis of environmental factors affecting community composition, but intercorrelated temperature and plant composition gradients appear to be important determinants of geometrid communities on this relatively short elevational transect.

There are 13,634 vascular plant species known from New Guinea (Camara-Leret et al. 2020), representing 4.0% of the 342,953 known species worldwide (Govaerts et al. 2021). There are approximately 24,000 described species of Geometridae worldwide (Murillo-Ramos et al., 2019), which would predict 960 known species from New Guinea, again assuming the 4% share of global diversity for geometrids. This would be comparable

to the 1,080 species of geometrids known from the much better-studied island of Borneo (Beck et al. 2010). However, the species pool of geometrids in New Guinea is certainly larger, considering that our sampling across just two altitudinal gradients yielded a total of 1,317 known and undescribed species of geometrids. Other rainforest elevation gradients, particularly complete rainforest elevation gradients reaching the tree line in the Saruwaged-Finisterre Mts, represent sampling priorities for further study of the geometrid fauna as well as the ecological factors that determine their communities (Beck et al. 2017).

Detailed baseline data on insect communities along elevational gradients are also essential for studying the effects of climate change on insect communities. Indeed, one of the few such studies available from tropical rainforests is a study of moth communities along an elevational gradient at Mt Kinabalu (Chen et al. 2009). Another key problem in tropical ecology that requires time-series data on insect communities is whether insect abundance is declining in tropical ecosystems as it is in temperate ecosystems, particularly in Europe (Lamarre et al. 2020).

Author contributions

RL, SI & PKA lead data collection in the field. PST and RL sorted the data and managed data storage. PST and VN conceived the idea, designed the project, analyzed the data and wrote the draft.

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Supplementary Information
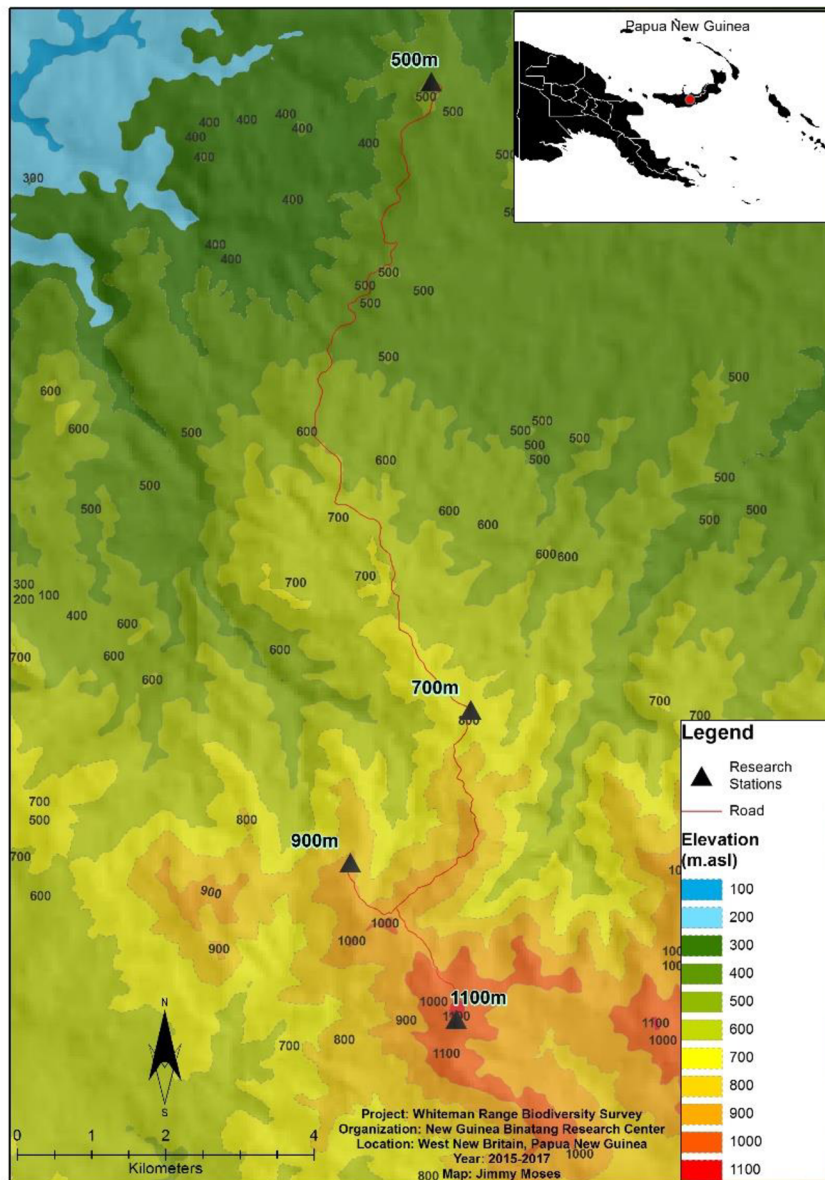
Figure S1. Map of the study sites at the Whiteman Range at four elevations: 500, 700, 900 and 1100 m asl. Insert shows the location in New Britain Island, PNG. © J. Moses

Table S1. Study location and the forest type

Elevation (meters-above-seal-level)	GPS Location	Forest Type
500	S05 88 215, E150.52 460	Lowland rainforest
700	S05 96 312, E150. 52 721	Lowland rainforest
900	S05 97 735, E150.51 894	Lower montane rainforest
1100	S05 59 686, E150 31 525	Mid montane rainforest

Figure S2. Light trapping method used for the survey (S. Ibalim collecting moths at 1100 m asl.). © P.K. Amick.

CHAPTER III

Biodiversity conservation with Indigenous peoples in tropics

Toko, P. S., Dem, F., Cámara-Leret, R., Martins, D. J., Philip, J., Matapi, U., West, P. & Novotny, V. (submitted to *Nature*, revision requested) (Manuscript)

Biodiversity conservation with Indigenous peoples in the tropics

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Abstract

Tropical biodiversity conservation is in crisis and requires new approaches that include Indigenous peoples who have long inhabited most tropical "wildernesses." The historical impact of Indigenous peoples on biodiversity has been mixed: while pre-agricultural communities caused the extinction of many megafauna and island species, swidden agriculture created sustainable, biodiverse landscapes alongside degraded landscapes. Today, many Indigenous communities are undergoing rapid change, combining traditional with new ways of life in the globalized world. Their conservation strategies of the past may no longer work today. In the tropics, Indigenous communities often view conservation differently than governments or NGOs, namely as a path to economic development that competes with alternative land uses. Logging can be attractive to remote communities if it brings roads that provide access to markets and services. The increasing threat of land conversion to agricultural use could severely limit biodiversity while providing economic benefits that are difficult for conservation projects to achieve. Payments for ecological services and conservation outcomes could potentially be viable conservation measures. Overall, tropical conservation remains unsustainable because it continues to be managed from overseas and lacks local public and political support. Paraecologists can link Indigenous and scientific knowledge systems and work with internationally supported local biologists to provide Indigenous leadership in building locally sustainable, science-based conservation.

Indigenous peoples and biodiversity conservation crisis

Tropical biodiversity is in a crisis, caused by the growing human footprint[1,2] and by inadequate conservation efforts that remain underfunded, inefficient, and of low political priority[3-5]. Many endangered tropical ecosystems have long been inhabited or even managed by Indigenous peoples[6] who are often considered role models for conservation[7]. While biodiversity conservation has been supported by detailed Indigenous knowledge of the natural world and sustainable resource use guided by traditional Indigenous practice [8,9], Indigenous ethnobiological knowledge is rapidly disappearing[10] and traditional lifestyles, attitudes, and practices related to conservation are also changing[11]. Where Indigenous peoples are the majority of the population and have recognized land rights and thus could make conservation decisions[3,12], as in many Melanesian countries, the conservation record remains poor[12] because conservation is seen as a pathway to economic development, in competition with alternative land uses[11]. In contrast, where the Indigenous people are in the minority, as in the Amazon, conservation outcomes are often excellent[13]. In sub-Saharan Africa, Indigenous conservation outcomes vary widely. Overall, the current and potential future role of Indigenous peoples in conservation continues to be hotly debated.

Indigenous peoples (i.e., peoples with distinct identity and culture, self-identification, historical continuity and strong connections to natural resources that either dominate or are marginalized in society[14]) are important to the future of tropical biodiversity. There are approximately 476 million Indigenous peoples, representing 6% of the world's population[15]. They have rights to or manage over 38 million km^2 of land in 40% of all terrestrial protected areas and ecologically intact landscapes[16,17] which harbour numerous threatened species[18]. Indigenous land rights are, therefore, a key issue for biodiversity conservation.

Land tenure systems in the tropics range from those that incorporate Indigenous peoples' rights and ecology in a few, mostly Melanesian,

countries[3,19] to those that exclude them, often as a legacy of colonial history. Customary land tenure is often defined for kinship groups rather than individuals[19,20], and information about land boundaries is passed orally between generations. This tradition lends itself well to the use of land for hunting and horticulture, but not for large-scale projects ranging from conservation to industrial logging or agriculture that span the lands of multiple Indigenous groups.

Melanesia is an instructive region to study Indigenous attitudes toward conservation and alternative land uses because most Melanesian countries legally protect customary land rights[21]. Unlike customary kin ownership, registration of land with individual land titles remains controversial. It allows for the economic mobilisation of land (e.g., as collateral for bank loans, leases, or sales)[22], but also increases the landless population at risk of poverty[23]. In Papua New Guinea (PNG) this led to the creation of more culturally appropriate voluntary community land titles[24], but such land incorporation did not yield economic success[23]. Most of the land in PNG therefore remains without formal title and is therefore unavailable for government conservation or commercial agriculture projects.

In tropical America, Indigenous peoples whose customary lands are not legally recognised are likely to oppose logging as a threat to their de facto land use, but this resistance is often ineffective. Land titles in such regions, such as the Amazon, can therefore benefit forest conservation[25] and curb deforestation[26]. In sub-Saharan Africa, Indigenous populations with subsistence livelihoods, such as pastoralism, often do not have formal land titles[27]. In Kenya and other free market countries, there are competing land tenure claims that are often resolved through land division and fragmentation, which has negative impacts on migratory Indigenous communities, especially pastoralists, and wildlife[28]. Hunter-gatherer communities have struggled to retain or gain rights to the land they use, which is usually controlled by the state[29].

Overall, land titles can lead to more economically rewarding alternatives to conservation while also facilitating new conservation approaches such

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as payments for ecosystem services[30,31]. They empower Indigenous peoples and open pathways to economic development, at the same time (i) increasing the economic value of land, triggering thus land disputes, (ii) requiring political representation of communities, leading to power struggles and increased inequality, and (iii) requiring consensus on land use at a spatial scale that often goes beyond traditional political alliances[20,21].

Indigenous conservation ranges from community-based agreements to government-designated protected areas[24]. Indigenous communities often face a trade-off between the degree of control they have over protected lands and the socioeconomic benefits they receive. For example, landowners in PNG receive no financial compensation from the government for committing to conservation, while retaining full control over their land (Table 1). Newly proposed legislation would provide conservation royalties in exchange for government oversight of land use, a proposal that is unlikely to be acceptable to most Indigenous communities.

Government-led conservation in the tropics includes many "paper parks" that are poorly funded and managed[32]. In the past, national parks, as areas free from human interference, have often driven Indigenous peoples off their lands[14]. Indigenous peoples therefore often resisted conservation and sometimes continued to use protected resources illegally[33]. Increasing concern for Indigenous peoples' rights led to new approaches to conservation. In the Colombian Amazon, Special Management Regimes put Indigenous people on an equal footing with the National Parks Authority in protected areas on Indigenous lands[34]. Protected areas in Africa benefit from the participation of local people in their management[35]. In Kenya, community conservation areas, including those of Indigenous peoples, exceed the size of formally protected areas[36]. Indigenous conservation activities have increased over the past decade, but the distribution of economic benefits from these activities remains contentious and can either alleviate or exacerbate local conflicts[37]. Conservation also benefits Indigenous peoples through integrated conservation and

development (ICAD) programmes[35,38,39]. Some critics see ICAD projects as examples of "deep colonisation" that limits Indigenous control over land to prescribed economic and lifestyle options compatible with conservation and call for abandoning the "exclusionary" approach to conservation and delegating biodiversity management to Indigenous people[14]. Although land titles have been an effective conservation tool in some Indigenous communities[25] and Indigenous peoples' participation in conservation management is generally beneficial, the assumption that Indigenous peoples are by default biodiversity-friendly landscape managers[6,14] as discussed below, is overly optimistic.

Tropical wilderness or domesticated landscapes?

Tropical rainforests were considered pristine "wilderness" by early European naturalists[40], although >90% of tropical forests have been inhabited by humans in the last 10,000 years[6,41]. Indigenous peoples have been variously viewed as threats or stewards of biodiversity. The initial expansion of humans out of Africa caused a severe loss of megafauna through hunting on all other continents[42]. This legacy persists today as many ecological functions of extinct megafauna remain unfulfilled[43]. In addition, oceanic islands in the Pacific lost >1,000 endemic bird species to newly introduced predators and hunting, largely before first European contact[44].

Hunting remains widespread in Indigenous communities, and is practiced by 39% of households[45], but mainly for subsistence consumption, which contributes little to household income[45] and is easily replaced by alternative benefits[5]. In PNG, hunting of endangered tree kangaroos declined when higher conservation-linked prices were introduced for locally produced coffee beans[46]. Wildlife meat markets in cities can increase hunting intensity and profitability in the surrounding landscape, creating "empty forests"[47]. The city of Manaus, for example, causes a "defaunation shadow" and overfishing on 1000 km of the Amazon[48].

However, interest in hunting is declining among Indigenous youths who see education and political leadership as more important sources of prestige[10]. In some Indigenous communities, sustainable hunting may serve as a motivation for forest conservation, similar to the first European reserves[49].

The invention of horticulture has had an increasing impact on tropical vegetation over the last 8,000 years and may even have increased atmospheric CO_2 concentrations through deforestation[50]. The impact of early horticulture on tropical forests has been underestimated, especially in the Americas, where pre-Columbian populations collapsed after European conquests, primarily due to new diseases[51]. The collapse caused vegetation to re-grow on >50 million hectares of land, causing a decline in atmospheric CO_2 between 1570 and 1620 that has even been proposed as a marker for the beginning of the Anthropocene[52]. Only recently has the extent of "domesticated forests", created by removal of non-beneficial plants, protection of useful plants and selection of their phenotypes, fire management, and soil improvement[53] been recognized in the Amazon[54,55] and elsewhere in the tropics[50].

The density of hunter-gatherer populations is determined by the net primary productivity of vegetation, except in the productive lowland tropics, where it is limited by pathogens[56]. The density of current horticultural populations in lowland rainforests remains low[57], possibly also due to density-dependent mortality from malaria and other parasites and pathogens[58]. The impact of these populations may have been less than natural disturbance rates in lowland rainforests. Population densities of one person per km^2 and 0.1-0.6 ha of land used per person per year[59] result in annual deforestation of <1% of the area by swidden horticulture, compared to the typical range of 1-2% due to natural causes[60].

The impact of horticulture at higher elevations was more severe[12] reflecting the higher population density that peaked in the tropics at >1,500 m a.s.l.[57], and the slower recovery of the forest after disturbance. Cloud forests in the Andes were cleared more rapidly in pre-Columbian times

than by cattle ranching after 1950[61]. In the mountains of New Guinea, locally invented horticulture[62] has produced two contrasting landscapes: a productive and species-rich agroforestry system of N-fixing *Casuarina* trees, crops, grasslands, and forest fragments that has been sustainable for more than a thousand years[8], and economically unproductive, species-poor grasslands established before first colonial contact with stone tools that represent a rainforest successional stage blocked by repeated, mostly human-caused fires[63] (Supplementary Fig. 1).

The contrast between these human-influenced landscapes in the highlands and the species-rich but sparsely populated rainforests in the lowlands suggests that lowland biodiversity is maintained not by the active management and stewardship of the ecosystem by Indigenous peoples, as has been argued[7], but because of the limited impact of their horticulture on lowland rainforests, resulting from low population density combined with rapid forest regeneration after disturbance. Despite the presence of humans, there are extensive wilderness areas where "ecological and evolutionary processes occur with minimal human disturbance," and these areas are experiencing catastrophic decline[1].

Indigenous communities are changing rapidly, so even resource conservation strategies that were successful in the past may not work today. Interaction between Indigenous communities and their natural environment has been controlled by local prohibitions on certain behaviours[64,65]. Many of these prohibitions on resource and habitat use function similarly to environmental protection laws today[65,66], even though the terms 'conservation' or 'biodiversity' do not appear in Indigenous languages[67]. These concepts are rooted in traditional beliefs and seasonal restrictions (Box 1) but are eroded by more recently introduced religious and other belief systems. Locally developed, community-supported regulations have sustained resources for centuries, but they are being disrupted under changing social conditions[68].

Many Indigenous populations have not yet completed the demographic transition and have been growing rapidly for >50 years, often in

biodiversity hotspots[69]. In Amazonia, the Indigenous populations that survived postcolonial collapses have recovered rapidly[70]. The sub-Saharan Africa has experienced profound changes in population, land tenure and land use patterns over the past five decades[71]. PNG's population doubled between 1975 and 2000. This led to a 58% increase in land used for swidden horticulture[72], making it as important a cause of forest loss as commercial logging[12]. Swidden horticulture remains widespread in the tropics[73,74], where it is an important cause of forest degradation. Improving its low yields[75] through fertilizers and other technologies has been proposed as a "land-sparing" policy approach to slowing deforestation. While such intensification may improve farmers' diets and economies, it rarely leads to better forest conservation. It may even have the opposite effect, known as the Jevons paradox, when higher economic returns from agriculture lead to its expansion[76]. Such an undesirable outcome may be less likely in Indigenous communities with secure land rights[55]. While replacing swidden cultivation with more intensive farming systems tends to increase incomes and improve health and education, it also leads to more conflict and inequality in farming communities[73]. For the environment, such a transition tends to reduce forest cover, biodiversity, and soil fertility[73].

Striving for conservation and/or development?

The assumption that Indigenous communities will conserve biodiversity if only given the opportunity has not been consistently true[77]. Conservation projects often suffer from conflicting priorities and expectations between Indigenous communities, governments, and local and international NGOs[3,78]. Holt[79] noted that cultural conditions compatible with biodiversity conservation, i.e. low population density, subsistence lifestyles, and limited use of technology, are precisely the conditions under which conservation practices are unlikely to emerge. Many Indigenous communities see biodiversity conservation as a pathway to economic development rather than a means of isolating the community from

markets[80] (Table 1). Non-economic approaches to conservation based on the continuation of independent traditional lifestyles and thus traditional controls on sustainable resource use have often failed, at least in PNG[11,81].

Indigenous communities living in remote areas with no land use options other than subsistence horticulture and hunting are almost always willing to support conservation because their opportunity cost of conservation is close to zero. The calculation may change if alternatives to conservation, such as logging or conversion of land for agriculture, become feasible[11]. Globally, deforestation rates are correlated with economic returns[82]. There is a dilemma of whether to invest in conservation in remote locations where the need for economic benefits is greatest, or in more accessible areas where the investment will have the greatest conservation impact[83]. Currently, protected area allocation is based primarily on low population density and poor accessibility, which minimizes risk but also reduces the net conservation effect[84]. As wilderness areas decline, conservation of partially disturbed areas, secondary forests and Indigenous-led restoration will become increasingly important for the future of tropical conservation[85] (Fig. 1).

Overall, contact with the market economy has had mixed effects on the Indigenous peoples' well-being and attitudes towards conservation[86]. Indigenous communities in PNG value protected areas on their land for their biodiversity, clean water, and spiritual significance, but also expect conservation to bring services, such as health, transportation, education, and employment[87] (Table 1). However, conservation projects often struggle to provide sustainable economic benefits that would make them competitive with alternative land uses[14]. Conservation projects are more likely to succeed in Indigenous communities with secure land rights and good governance. Otherwise, their economic benefits could have the perverse effect of attracting people to protected areas[38].

The economic benefits of conservation range from indirect to direct. Indirect benefits include support for local economies or improvements in health, education, or transportation in return for conservation, while direct

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benefits include performance-based payments for conservation[88]. Income generated by biodiversity research and monitoring, ecotourism, or conservation-certified products depends on conservation, while projects unrelated to it, such as agriculture or community forestry, may even compete with conservation if expanded (Supplementary Fig. 2). Agricultural projects can transform the livelihoods of subsistence farmers into organized laborers growing cash crops and result in negative social consequences[68]. Payments to compensate landowners for conservation, or "conservation royalties" could be collected by the government (e.g., as a levy on timber exports), by conservation NGOs (from donors), or by companies as offsets to compensate for their ecological footprint (Fig. 2). These payments could also serve as compensation for ecological services provided by conservation, such as carbon sequestration under REDD+ or payments for biodiversity outcome programmes[89].

Payment for ecosystem services represents a new, potentially viable economic alternative to timber extraction[90]. However, such projects may shift the balance of control over land between governments and Indigenous communities[91,92]. There is a potential conflict between local land rights and the nationally pledged mandate to mitigate climate change. The carbon sequestration efficiency by forests also tends to be uncorrelated with their biodiversity. At the same time, international markets for ecosystem services can also correct situations where conservation is beneficial for Indigenous communities but financially detrimental to national governments[93]. Insufficient participation of Indigenous peoples and NGOs in design, lack of trust, and uncertain legal frameworks were reported for REDD+ projects in 11 Asia-Pacific countries[94]. Some of the REDD+ offers to Indigenous communities also come from unscrupulous or fraudulent traders aptly named "carbon cowboys"[95]. The new concept of payment for ecosystem services can be difficult to grasp locally and inflated lead to the cycle of "hype, hope, and disappointment" cycle[96]. However, payments for conservation outcomes have the potential to cover the opportunity costs of conservation, especially if the Indigenous communities are allowed to co-

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design and manage such projects, reaping their benefits while retaining control over their lands[30,97].

Forest conservation often must compete with logging. In Indigenous communities with secure land rights, logging can bring financial benefits, but in the words of one Solomon Islands' community "the happy hour became the hungry hour" after the short-lived bonanza of royalties from logging ended and their sustainable lifestyle was disrupted[98]. In PNG, logging often triumphs over conservation[11]. This reflects the mostly poor performance of conservation, as the income required for successful conservation remains low in PNG Indigenous communities (Table 1). For example, the Wanang Conservation Area, on land co-owned by one of the authors (JP), accounts for ~10% of the land within a logging concession where the remaining communities have opted for logging[99] (Fig. 2). Community-based forestry can be an environmentally and socially preferable alternative to commercial logging, but often struggles with low quality and low volume of production, poor access to markets[21,100], and difficulties in certification for sustainable logging[101].

In theory, sustainable harvesting of non-timber forest products could be more economically lucrative than logging[102], but in practice it is rarely economically viable due to lack of access to markets and unpredictable and low production volumes. Rubber, one of the most economically successful rainforest products, was originally harvested from natural forests, but rubber production has shifted to more efficient plantations that now compete with rainforests for land[103]. This is a risk to any successful forest product. In addition, customary land tenure is no guarantee of sustainable harvesting, especially for new products without traditional harvesting techniques. In PNG, harvesting of eaglewood (a resinous product derived from a fungal infection of *Gyrinops* trees) quickly led to large-scale felling of trees by Indigenous landowners[104] (VN, pers. obs.). However, the Kayapó people of Brazil have successfully combined mahogany extraction with conservation, preserving the last large forest reserve in southeastern Amazonia[105].

While logging and swidden horticulture are the main causes of deforestation in the Pacific and Africa, rainforests in the Amazon and SE Asia are threatened primarily by land conversion to agricultural land[106]. Conversion of rainforest to pastures or plantations severely reduces biodiversity but also provides a regular income that can be attractive to small farmers. The impact of agriculture on biodiversity can be mitigated directly through biodiversity-friendly practices such as shade coffee, or indirectly through intensive crop production on only a portion of land explicitly associated with an area of conserved natural ecosystem, such as conservation coffee[46].

The ambiguous relationship between roads and conservation illustrates the double-edged impact of development on conservation by Indigenous peoples. Roads fragment natural ecosystems[107] and accelerate deforestation[108], but they also provide access to markets, jobs, and education[109]. Distance to road correlates positively with economic status and negatively with traditional lifestyles in Indigenous communities[10,110]. Indigenous communities with secure control over their land, as in PNG, view roads as an important benefit that may come from logging or possibly conservation[78] (Table 1, Supplementary Fig. 3). This attitude contrasts with academic exercises in road optimization which, for example, propose the unrealistic scenario that no new roads should be built in New Guinea[111] and criticize modest expansion of road network in PNG[112]. The negative impacts of roads can be mitigated by secure land tenure that reduces the uncontrolled influx of settlers into rainforest areas accessed by roads, as is the case in PNG[11] but not in the Amazon[108] and Africa[113].

In South America there are approximately 200 Indigenous groups with 10,000 individuals living in voluntary isolation or with sporadic contact[114]. The isolated groups have a disproportionate impact on biodiversity conservation. For example, the Indigenous land of Valle do Javarí in the Brazilian Amazon was recognised to protect isolated Indigenous peoples and now covers an area the size of Portugal. The expansion of Colombia's

largest national park, Chiribiquete, was also partially justified by the presence of isolated communities[115].

The degree of openness to outsiders and their ideas varies among Indigenous cultures. The world's last large-scale first contact between a million Indigenous peoples and Australian colonial patrols took place in the New Guinea Highlands in and after 1932 and was characterised by a keen interest in outsiders by Indigenous groups[63]. In contrast, the Pirahã in the Brazilian Amazon have yet to adopt external ideas and technologies or convert to Catholicism despite 200 years of missionary efforts[116]. Mobile phones are now reaching many remote communities before roads, intensifying information exchange with the outside world[117]. Changing Indigenous lifestyles may undermine traditional controls on sustainable resource use, but they may also bring new ideas for conservation[118].

In summary, an Indigenous rainforest-dwelling community with subsistence horticulture can take several paths to higher economic status, including [i] community and then government-sponsored conservation, [ii] community or industrial logging, [iii] smallholder or plantation-scale cash crop agriculture, or [iv] mining (Supplementary Fig. 4). The pathways other than conservation result in varying degrees of biodiversity erosion. The experience from PNG, a country where Indigenous communities can decide their own path, shows the importance of conservation being competitive with the alternative pathways to development. Selective logging is currently the most common competitor to conservation, but land use for agriculture is the greatest future threat in PNG, and the greatest current threat globally[11]. Involving Indigenous communities in conservation decisions is critical to the sustainability and future legitimacy of these decisions.

Indigenous ways of knowing, science and conservation

Some scholars have argued that biological knowledge accumulated by Indigenous societies can be considered an "alternative way of knowing" to

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the scientific tradition. Sillitoe[119] contrasted the intuitive, holistic, and subjective knowledge systems of Indigenous peoples with the analytical, reductionist, and objective nature of science. We do not believe this dichotomy is meaningful and prefer to focus on the ways in which Indigenous knowledge and scientific knowledge can be combined to create more complex and complete understanding of the natural world.

There are approximately 7,000 Indigenous languages, each with botanical and zoological taxonomies of varying complexity. A typical Indigenous classification includes hundreds of plant and vertebrate species, most of which are defined in accordance with the modern concept of species, although not necessarily matching them one-to-one with the taxonomic species[120]. Indigenous people's intimate knowledge of the ecology and behaviour of bird and mammal species often surpasses that of professional biologists[64,121] and makes Indigenous people excellent parataxonomists and paraecologists in biological research that links Indigenous and scientific knowledge systems[122] (Fig. 3). Conservation strategies could also benefit from Indigenous ecological knowledge[123]. For example, Novera & Kark[87] outline a conservation approach that combines traditional ecological knowledge and practises with science to protect biologically and culturally important ecosystems under customary tenure. However, some traditional belief systems do not recognise the ability of humans to manipulate and thus harm nature. If animal populations are controlled by spirits, the assumption that hunters can drive them to extinction seems presumptuous[110].

Rainforest communities use hundreds of plant species, most of them for medicinal purposes. Most of these plant uses have never been recorded in writing. For example, there are ~20,000 records of a particular plant species used by a particular language group from New Guinea[124]. However, there are ~1,000 language groups in New Guinea, each using 200-500 plant species[125], so ≥90% of plant uses remain undocumented. Nearly half of the world's languages are at risk of extinction, while declines in language proficiency and traditional lifestyles are the main causes of the

rapid loss of ethnobiological knowledge we are currently experiencing[10,126].

The use of Indigenous medicinal and biodiversity knowledge in bioprospecting has been proposed as a mechanism to pay for biodiversity conservation but has also been seen as exploitation of Indigenous people. The small size of Indigenous groups, typically a few thousand people[10], combined with a strong placebo effect of Indigenous healers and imperfect oral transmission of information between generations suggests a rather inefficient system. The lack of consistency between medicinal uses of the same plant species by different communities[127] suggests that many of the plant uses have only a placebo effect. On the other hand, differences in floristic composition between cultures may have resulted in a different plant being used effectively to treat a particular ailment in each culture.

Natural products continue to be an important source for drug discovery. From 1981 – 2014, most approved drugs were from natural products[128]. However, the promise that rainforests are humanity's "medicine chest," which is also used to justify their protection, has not been fulfilled[129]. Pharmaceutical research spends very little on bioprospecting[130] compared to alternative approaches to drug discovery such as combinatorial chemistry and structure-based drug design[131]. For example, International Cooperative Biodiversity Groups (ICBGs), which aim to integrate drug discovery, bio-inventory, conservation, and expertise building in developing countries, have been successful primarily in building research capacity[132]. The legal and political problems of commercializing Indigenous knowledge[132] and some high-profile cases of misuse of this knowledge have led some Indigenous communities to impose a research moratorium on their lands[133], but also pharmaceutical companies to exclude Indigenous knowledge from their bioprospecting strategies[134]. The high expectations of bioprospecting motivated the Nagoya Protocol on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization[135]. It has been widely criticized for conflating commercial and non-commercial research, discouraging

participation in research in the Global South, including by Indigenous communities, and thus promoting global inequality rather than mitigating it[136].

Tropical countries tend to be economically underdeveloped and invest little in biodiversity research and conservation[137]. This is one of the reasons why conservation research[4] and action[138] are not taking place where they are most needed. Lack of local biological expertise is a major obstacle to biodiversity conservation in the tropics, where biological research is mainly conducted by foreigners[139,140]. Tropical scientists often face high teaching loads, low wages, and poor access to information and equipment, which undermines their academic careers[140]. This may explain why important taxonomic projects such as Flora Malesiana or Flora of Tropical East Africa are dominated by foreign botanists[141,142]. A strong academic community is an important first step in promoting conservation to the public and national policy[143]. Many tropical countries are eager to build their own research capacity, as evidenced by the recent call for more indigenous research from countries in the Congo Basin[144].

There is a need for more equitable collaboration between extratropical biologists and their colleagues and communities in the global South[145]. Indigenous communities can play an important role in biological research as their lands often harbour great biodiversity and many community members can become paraecologists, research assistants, conservation rangers, or students[122]. These roles often merit co-authorship of research publications as well as adequate funding for local institutions[146,147]. Such collaborations can be very productive scientifically but require a significant upfront investment in training[122]. Many tropical countries with large numbers of young people and increasingly accessible university education offer opportunities for in-country expertise building, including in conjunction with rapidly growing citizen science platforms and natural history associations[148].

Collaboration between Indigenous communities and researchers from developing and developed countries must bridge cultural differences[149].

For example, knowledge in Indigenous communities may be considered a communal resource[67] and some Indigenous knowledge may be inaccessible to outsiders. There may be differences in how Indigenous communities and transnational biologists value biodiversity[150]. At the national level, willingness to spend money on conservation depends on GDP per capita, quality of governance, individualism, and power distance (willingness to accept hierarchies) - all parameters that often differ between the global North and South[151]. The current "collaboration gap" in tropical research needs to be addressed to achieve sustainable, locally supported conservation in the tropics. In particular, intellectual and financial participation of local stakeholders should become standard practice in biological research in the tropics. Only 5% of the supermarket price of coffee beans goes to the farmers in the tropics who grew them[152]. Are researchers, or conservationists, better at sharing their budgets with their tropical counterparts?

Long-term monitoring is particularly important for ecological research, but also difficult to sustain without local support, which is often inadequately appreciated and funded[147]. New opportunities for monitoring by Indigenous paraecologists equipped with modern digital platforms are emerging[153,154]. Biodiversity inventory and taxonomy expertise, a potential strength of Indigenous communities, is declining globally[155,156]. This unfortunate trend could provide opportunities for tropical countries to become competitive in these fields by combining access to Indigenous lands for research with modern approaches to taxonomy[157].

In underdeveloped tropical countries, conservation NGOs offer an alternative to the largely absent state[78,118] (Table 1). International conservation NGOs bring expertise and funding to tropical countries, but also compete with national NGOs and universities for resources and the limited pool of local experts[158]. In some tropical countries, international NGOs have made themselves indispensable for the national conservation policies with their biodiversity data and expertise. However, conservation by international NGOs in the tropics can never be sustainable because of a

lack of local political support. Even after decades of operation, none of the international NGOs have ever left a tropical country because they put local conservation on a sustainable footing and were no longer needed[159].

The future of Indigenous conservation

The threats to biodiversity faced by Indigenous peoples in the tropics have changed over time, with the opportunity cost of biodiversity conservation gradually increasing. Traditional lifestyles based on swidden horticulture have often, though not always, resulted in sustainable and productive landscapes. When hunting and horticulture are no longer sustainable due to increasing population density, it is relatively easy to compensate with livestock, improved agricultural techniques, and new crops.

Indigenous communities faced with a choice between conservation and logging are in a more precarious position, as it is difficult for conservation projects to financially offset the opportunity costs of conservation. Indigenous communities in roadless areas are particularly vulnerable, as logging roads provide an important benefit by opening access to markets and services. Tropical conservation has largely failed to compete with logging, even in countries with secure Indigenous land titles such as PNG or the Solomon Islands. In many tropical countries, particularly in the tropics of the Americas and Asia, logging has been replaced by land conversion to agriculture as the main threat to tropical biodiversity[106]. This is particularly bad news for conservation, as land conversion has greater negative impacts on biodiversity than logging, while the economic benefits of agriculture are difficult for conservation projects to match. These trends suggest that biodiversity conservation in the tropics will come under increasing pressure. This will require new approaches, including payments for ecosystem services and conservation royalties, and much greater investment than in the past.

The greatest challenge for Indigenous conservation in general is to develop conservation strategies that support economic aspirations of Indigenous

peoples while considering changes in their lifestyles. Supporting Indigenous communities secure land rights and participate in the management and biological monitoring of protected areas that are economically viable will be central to tropical conservation in the 21st century.

Most Indigenous communities are exposed to the globalized world and combine traditional ways with new ones. Young people tend to value their own culture while absorbing much of the global flow of ideas. This often leads to a decline in Indigenous language skills, traditional ways of life, and ethnobiological knowledge that has historically developed in situ with little interaction with the outside world. This is particularly the case among the educated and urbanized segments of the Indigenous populations[10]. These changes may weaken traditional attitudes toward conservation as well as traditional methods of sustainable resource use. At the same time, Indigenous populations are being exposed to new ideas about conservation. The combination of traditional and new knowledge positions Indigenous communities to play a greater role in the global biodiversity research agenda. This agenda should include linking Indigenous knowledge and biological science to build strong local academic and human rights capacity, which is essential for sustainable conservation.

Most scenarios predict a decline in global population after 2050[160], with the majority of the population living in cities[161]. These trends, along with improved agricultural efficiency, could free up land for wildlife[162], as is already happening in Europe[163]. We live in a critical time as we approach the peak of pressure on tropical biodiversity and natural resources. Whether the magnificent and enormously information-rich biodiversity of the tropics survives this bottleneck depends largely on our current conservation choices. Indigenous peoples should play a prominent role in this process.

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Tables

Table 1 Key parameters of Indigenous protected areas in PNG

A selection of conservation projects in PNG for which detailed information was available. Protected areas in PNG are mostly exclusively indigenous areas that have not been legally recognized by the government. They protect ecosystems, primarily rainforests, rather than keystone species, from threats mostly resulting from commercial logging and swidden agriculture, rather than commercial agriculture. The median protected area is small, ~10,000 ha, with a low population density of ~0.1 persons per protected hectare. Protected areas are mostly managed by Indigenous peoples in collaboration with NGOs that also provides conservation-related funding and services instead of the government. Annual funding for conservation typically ranges from £0.25-2.5 per hectare and £2-10 per person. Most projects brought conservation-related businesses or education/health services to the community. Conservation often entailed research and monitoring, but not tourists. Road access remains the most important unmet community need and also the most important lost benefit that could have been provided by logging. The three inactive projects failed due to internal conflicts in the community (KCM, LRB), failure of ecotourism projects (KCM, LRB, MLA), and preference for logging as a source of income (LAK). The predominant cathegory is shown in red. See Supplementary Data for full names of protected areas and sources of information.

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Conservation area	cathegories [dominant option in red]				KCA	MCF	MEC	WCA	TMC	KWA	YUS	CWM	KCP	WCF	MGC	KWM	LRB	LAK	KCM	MLA
Conservation success rated on 0 - 10 scale, low: 0-3, medium: 4-6, high 7-10	low	medium	high																	
Legal form: indigenous, indigenous with governmental in process, governmental	ind	ind/gov	gov																	
Conservation duration: short (<20 years), long (≥20 years), failed	short	long	closed																	
Ecosystem protected: rainforests or marine	rainfor.	marine																		
Top threat to conservation: logging, swidden agriculture, indigenous hunting	logging	agric.	hunting	none																
Conservation focus on flagship species or entire ecosystem	species	ecosyst.																		
Conservation area size: small (≤10,000 ha), large (>10.000 ha)	small	large																		
Population impacted by conservation area: small (<0.1 ind/ha), large (≥0.1 ind/ha)	small	large																		
Remote area (travel to the nearest town ≤6 hours one way): yes or no	yes	no																		
Conservation management & enforcement: indigenous community alone, or with an NGO	ind	ind+NGO	ind+gov																	
Monitoring/research	yes	no																		
Funding/services delivery: indig. community alone, with an NGO, or the government	ind	ind+NGO	ind+gov																	
Conservation income per person and year: low (£<2), medium (£2-10), high (>£10)	low	medium	high																	
Conservation income per ha and year: low (£<0.25), medium (£0.25-2.50), high (>£2.50)	low	medium	high																	
Business projects brought by conservation, others, both or neither	conserv.	other	both	neither																
Services brought/improved by conservation: education, health, both or neither	educ.	health	both	neither																
Visits by tourists (>100 per year), researchers & students or neither	tourism	research	both	neither																
Top unsatisfied needs: roads, services (health, education, etc.), income opportunities	road	services	income	no data																
Top benefits missed due to conservation: roads, mining employment, or none	road	mining	none																	

Text Box 1.

Matapí Upichía Ecological Calendar (Amazonas, Colombia)

For the Matapí, the ecological calendar determines the schedule of conservation, protection, and maintenance of the territory. Culturally, it organizes the daily activities in distinct seasons:

- leerú yájõwa (worm season, Aug-Sep): The calendar begins when most plants are in bloom. It is the time of diseases and the infection with malaria is prevented by baths with certain plants, shamanic processes, and the consumption of certain foods. Restrictions include eating pineapple, sugar cane, and lulo (*Solanum sessiliflorum*), hunting, fishing, or felling trees (unless they belong to the chagra, the land to be cultivated). A time for clearing the undergrowth ("socolar"), logging (in August) and burning (September) to prepare the "chagra" and the season for building the maloca (indigenous roundhouse).

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- leerú yaaní (pineapple season, Oct-Dec): Pineapples bear fruit and the ritual pineapple dance (mawiru yaale) is performed to celebrate the abundance of the fruit. The time of gathering certain fruits, hunting and fishing, as long as these activities follow the ancestral prescriptions and the shaman's instructions.

- a'awanachá jeéná (harvest season, Jan-Mar): There is a peak production of fruits and their gathering is allowed without restrictions for a period of 15 days. Hunting is allowed without restrictions until the end of February, but is prohibited towards the end of the season, when the animals begin to reproduce. Season for the ritual dance of the pipirí palm (*Bactris gasipaes*).

- yawijá (winter season, Apr-Jun): Animals reproduce and hunting is completely prohibited. Harvesting of fruits such as punama (*Oenocarpus bataua*), pupé (*O. bacaba*), malakala (*Euterpe precatoria*), and yuchi (*Couma macrocarpa*) is allowed, but without cutting down the plants.

- luukamá (cold season, Jul): The last season of the calendar. Due to the cold weather, animals disappear, including the jaguar (*Pantera onca*). Only the fruits of species like itewí (*Mauritia flexuosa*) or tuupí (*Astrocaryum chambira*) are eaten.
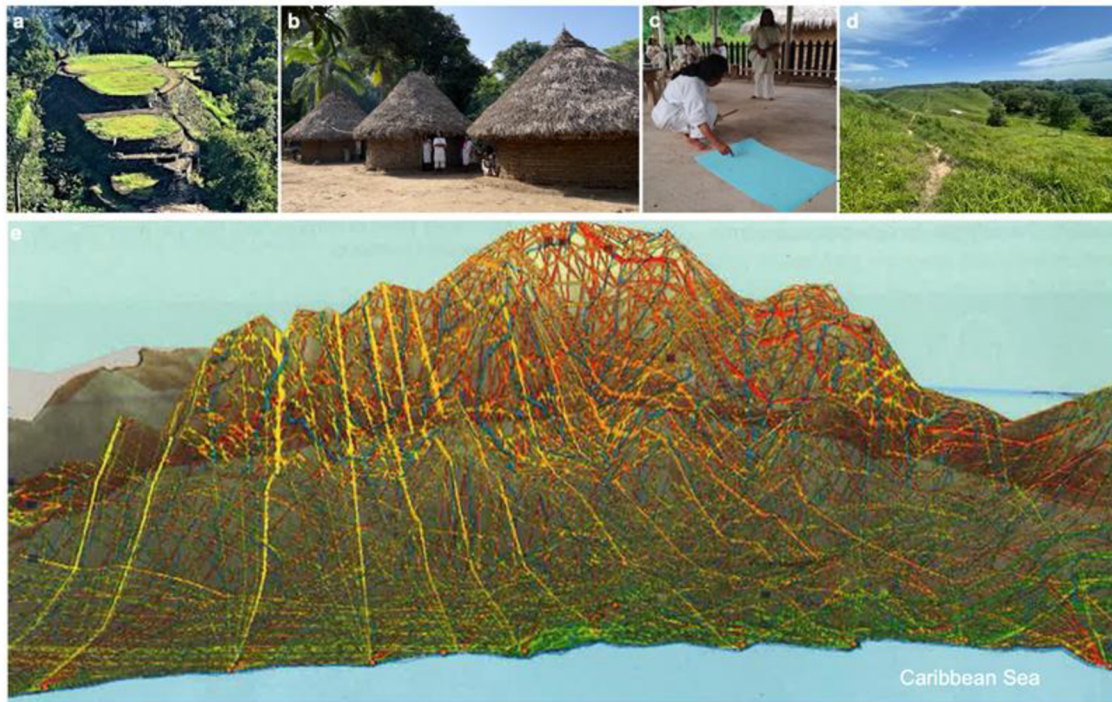
Figures

Fig. 1. Indigenous peoples restore the fabric of life. The Kogi of the Sierra Nevada de Santa Marta (Colombia) and their bold attempt to reclaim and restore their ancestral lands. The Kogi are related to the Tairona civilization that inhabited the archaeological site of Teyuna or the 'Lost City' with over a hundred mountain terraces connected by tiled roads (a). The Kogi survived the invasion of European and Colombian settlers by retreating to remote areas with low soil fertility (b). In recent decades with the support of NGOs they have strategically acquired portions of their ancestral territory in the Caribbean lowlands (c), which they are restoring (d) to bring back water to the Sierra, strengthen their traditional practises and livelihoods, and reconnect sacred sites as 'acupuncture' of the landscape to heal Mother Earth (e). Replicating such indigenous-led initiatives holds promise for the future of conservation. Photos: a-d, Tairona Heritage Trust; e, Organización Gonawindúa Tairona. 2018. "Shikwakala: el crujido de la Madre Tierra." ISBN: 9585763419.
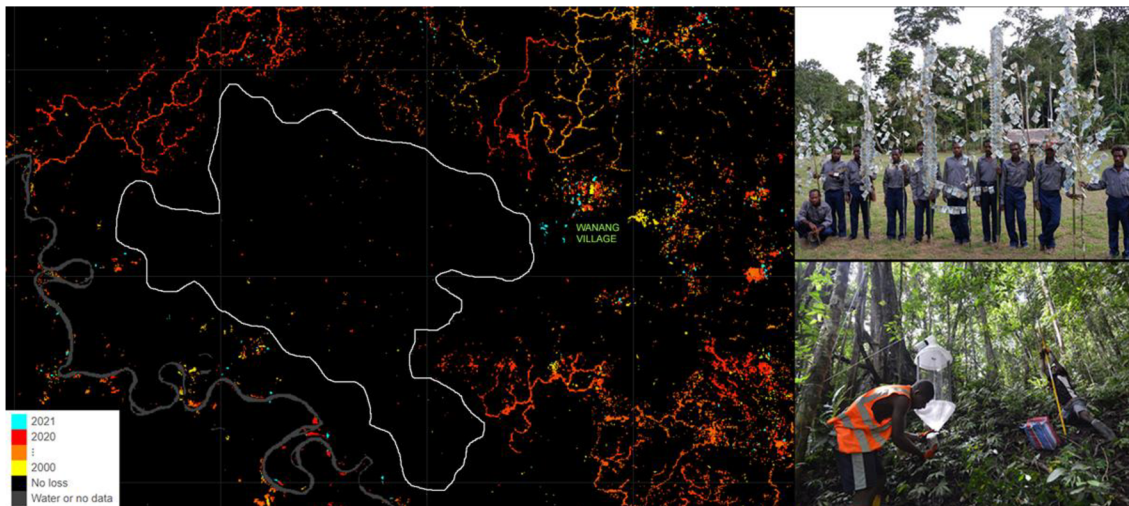
Fig. 2. Forest loss map[164] showing the Wanang Conservation Area (white outline) established by indigenous landowners from Wanang village (PNG) surrounded by selective logging (left); Wanang clan leaders receiving an annual payment for forest conservation (conservation royalties) (top right); and Wanang paraecologists studying insect communities (bottom right)[11]. Photos V. Novotny (top) and M. Leponce (bottom).
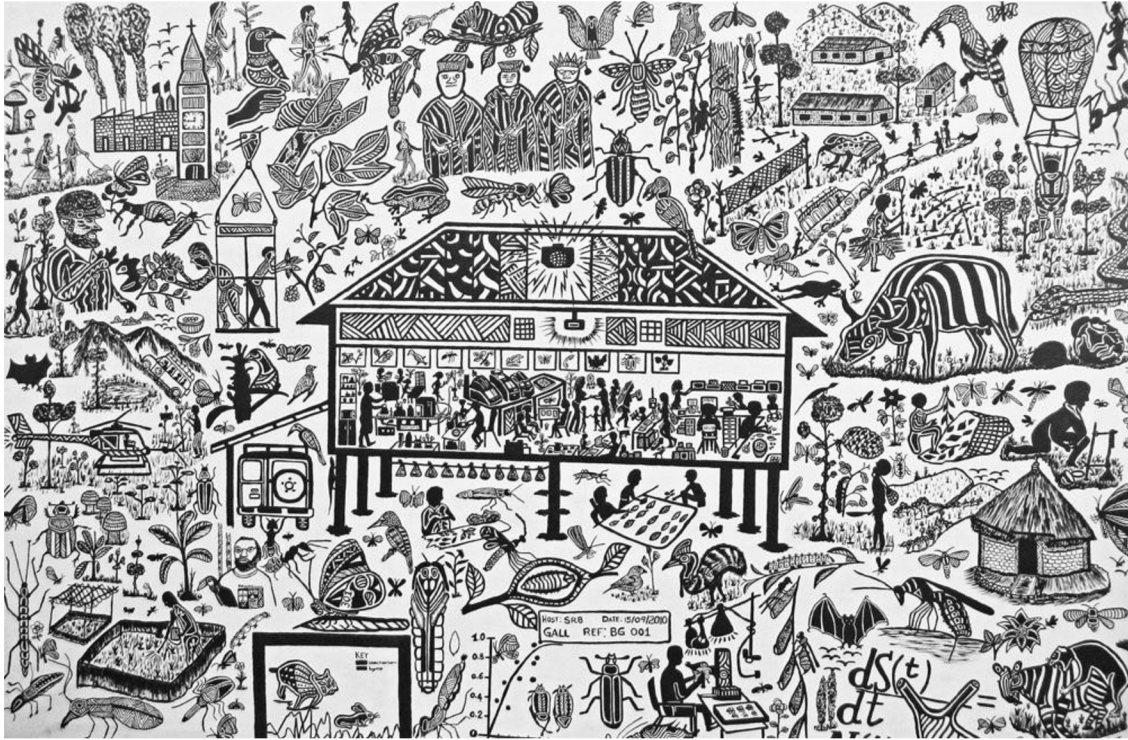
Fig. 3. Various ecological research projects involving researchers working with Indigenous paraecologists in PNG and Cameroon in local protected areas. Drawing by Benson Avea Bego, a self-taught Indigenous artist from PNG.

Supplementary Information

|		
Biodiversity	medium	low	high
Human footprint	medium	high	low
Economic productivity	high	low	medium

Supplementary **Fig. 1**. Landscapes formed (**A, B**) or inhabited (**C**) by indigenous peoples in New Guinea: a highland agroforestry (**A**), a highland anthropic grassland (**B**) and a lowland primary rainforest (**C**). Photo V. Novotny (**A, B**) and M. Leponce (**C**).
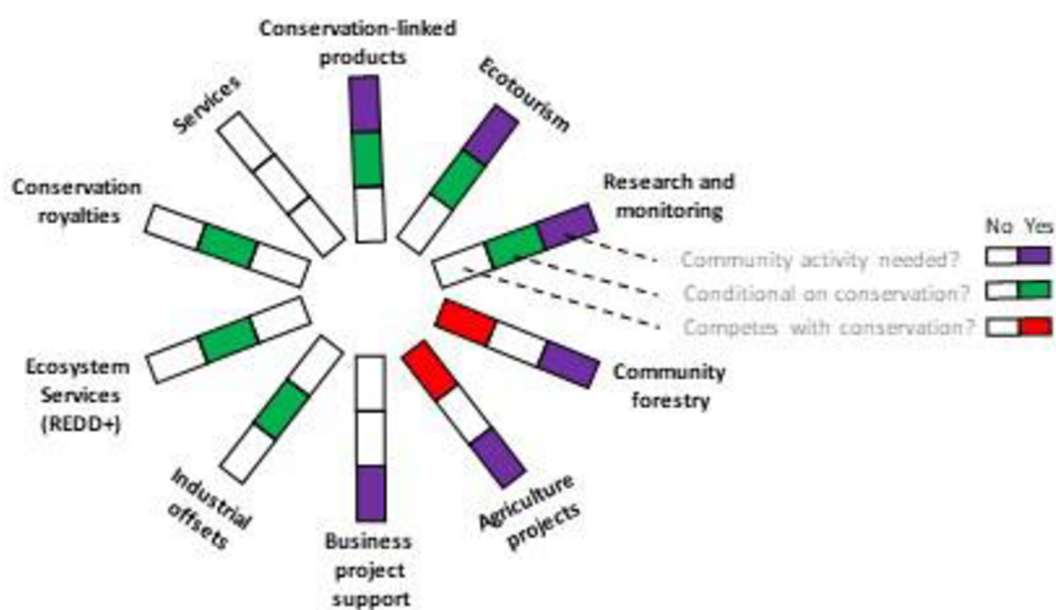
Supplementary **Fig 2**. Economic interventions in support of conservation, classified by [i] the activity required by the recipient community, [ii] the link to conservation, and [iii] the potential to compete with conservation.
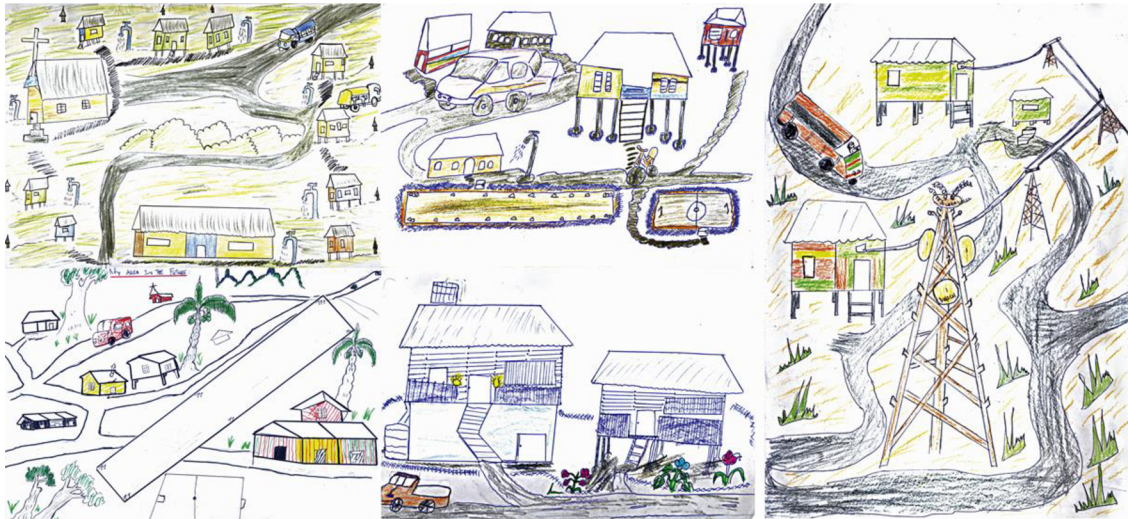
Supplementary **Fig. 3**. How children at a primary school in Yawan, a remote village in the indigenous YUS Conservation Area (PNG), envision the future of their village. Yawan has no road connection, no electricity or water supply, and no mobile phone signal, all developments that the children expect to see in the future. Note also the absence of any evidence of traditional lifestyles. These expectations are representative of many remote villages in PNG. Reprinted from Hubenakova & Soukup[165].
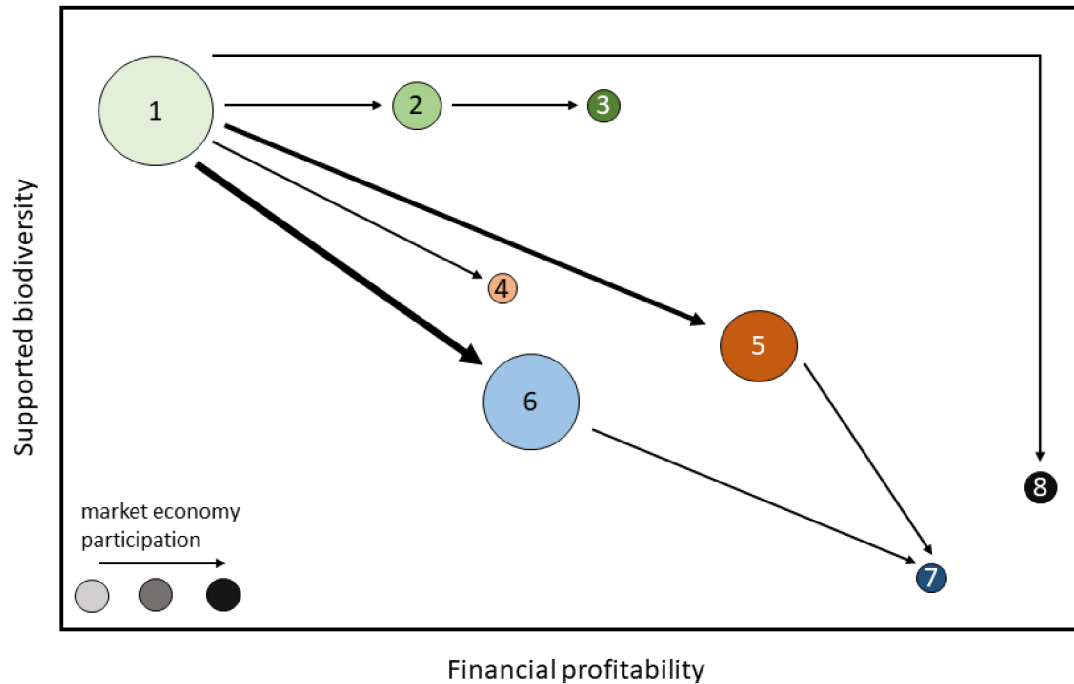
Supplementary **Fig 4**. Indigenous community development in PNG in relation to economy and biodiversity, including conservation (green), logging (brown), agriculture (blue) and mining (black): 1 – subsistence horticulture, 2 – Indigenous conservation, 3 – government conservation, 4 - community forestry, 5 - industrial logging, 6 – smallholder cash crops, 7 – plantation agriculture, 8 – industrial mining. The size of the bubbles reflects the number of communities, the thickness of the arrows the transition frequency, the colour shading the participation in the market economy. This is a conceptual scheme, not based on quantitative data.

Conservation areas, informants and data sources for Table 1

CWU - Crater Mt. Wildlife Management Area, S. Tiu

KCA - Karawari Cave Arts, F. Damnor

KCP - Karimui Conservation and Resources Management Programme, J. Anuabo

KCM - Karkum Community-Based Marine Resource Management Area, W. Magun

KWA - Kau Wildlife Area, F. Dem

KWM – Kamiali Wildlife Management Area, Peterson, A. & Rei., V. Management Effectiveness Tracking Tool: Kamiali, 16 pp. (UNDP PNG, 2016)

MCF - Manus Central Forest, A. Tejedor, J. Kuange, and P. Shrestha

MGC - Mt. Goplom Conservation Area, A. Tejedor, J. Kuange, and P. Shrestha

MEC - Mauberema Ecotourism and Conservation Area, M. Kerry

TMC - Torricelli Mountain Range Conservation Area, J. Thomas

WCA - Wanang Conservation Area, F. Damen and J. Philip

WCF - Whiteman Range Carbon Forest Conservation, P. Pose

YUS - YUS Conservation Area, L. Dabek

MLA - Madang Lagoon Reefs, J. Billy

LAK - LAK Conservation, Ellis, J.-A. Race for the Rainforest II: Applying Lessons Learned from Lak to the Bismarck-Ramu Integrated Conservation and Development Initiative in Papua New Guinea. (PNG Biodiversity Conservation and Resource Management Programme, 1997)

LRB - Lakekamu River Basin Project, Kirsch, S. Regional Dynamics and Conservation in Papua New Guinea: The Lakekamu River Basin Project. *The Contemporary Pacific*, **9**, 97-120 (1997) and Salafsky, N. Lessons from the field. Linking theory and practice in biodiversity conservation. *Biodiv. Cons. Network*, **1**, 1-11 (1999).

We thank the colleagues mentioned above for providing information on the protected areas that they are familiar with or managing.

SUMMARY

Thesis summary

Using the distribution of geometrid moths (Lepidoptera, Geometridae) as a model taxon, this thesis examines patterns of alpha diversity in local communities from different elevations, beta diversity along elevational transects, and landscape-scale gamma diversity on two different islands in Papua New Guinea (PNG). These rainforest studies, conducted in collaboration with local indigenous rainforest-dwelling people, also led to an analysis of the role of indigenous communities in rainforest conservation in PNG and at the global level.

In **Chapter I**, we analysed Geometridae community composition along the Mt. Wilhelm elevation transect from 200 to 3,700 m asl at Mt. Wilhelm in PNG. This is one of the most floristically rich areas in the world, with > 5,000 plant species per 10,000 km². We have examined the effects of elevational change on plant diversity and biomass, abundance and diversity of predators such as insectivorous birds, bats, and ants, and temperature on the species diversity, which reached a maximum at mid-elevation at 1,200 m a.s.l., likely as a result of increasing biotic and decreasing abiotic environmental favorability with increasing elevation. We documented that beta diversity increased with increasing elevation, contrary to the trend expected based on the Rapoport rule. Species fluctuation along the elevation gradient resulted in total geometrid diversity along the transect being 280% of the maximum local community diversity, quantifying the effects of elevation gradients on local diversity.

In the **Chapter II** we used sampling protocols from Mt. Wilhelm on a shorter elevation gradient in the Whiteman Range on New Britain Island, a geographically nearby oceanic island that does not share a common geologic history with Mt. Wilhelm. Species diversity of geometrid communities at the corresponding elevations on the Whiteman Range was similar to that on Mt. Wilhelm. The influence of island size on species diversity was not detected. There was a large overlap in species composition between Whiteman Range and Mt. Wilhelm, and population sizes of species common to both transects were correlated. This suggests

possible dispersal between the two ranges on short and long time scales. The total of 1,317 species documented for the two montane ranges suggests an exceptionally diverse geometrid fauna in the New Guinea region, probably even more diverse than that of Borneo. We have also demonstrated the usefulness of COI barcoding for defining species concepts along elevational gradients, particularly within a very species-rich fauna such as that of New Guinea.

Finally, in **Chapter III** we have moved from ecological studies to conservation challenges – an issue of importance both to the people who live in rainforests and to the conservation of global biodiversity. Large areas of rainforest are located in some of the most underdeveloped countries in the world, making their conservation a complex socioeconomic undertaking. Many indigenous peoples living in rainforests are often portrayed by international conservation organizations as born conservationists who prefer their traditional way of life while they themselves seek economic development. This discrepancy between expectations and reality is one of the reasons why rainforest conservation has not been very successful, even in countries like PNG where indigenous peoples are legally recognized landowners. Analysis of this situation suggests ways to achieve the goals of biodiversity conservation, preservation of traditional cultures, and socioeconomic development in tropical rainforest communities.

CURRICULUM VITAE

<h1>Curriculum Vitae</h1>

PAGI TOKO
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EDUCATION
2016 – Present Ph.D in Entomology, University of South Bohemia, Czech Republic
2009 – 2010 M.Sc in Biology, University of Papua New Guinea,
2007 – 2008 B.Sc in Biology, (Honors, First Class), University of Papua New Guinea
2004 – 2007 B.Sc in Biology, University of Papua New Guinea

EMPLOYMENT
2023 Board Chairman, New Guinea Binatang Research Center
2013 – 2016 Deputy Director, New Guinea Binatang Research Center, Papua New Guinea
2016 – Present Researcher, Institute of Entomology, Biology Center, Czech Academy of Science, Czech Republic

INTERNATIONAL APPOINTMENT
2016 – Present, PNG country representative, Association for Tropical Biology & Conservation (ATBC)

INTERNATIONAL LAB VISIT
2019 Two months at Zoologische Staatssammlung München, Germany under Dr Axel Hausmann

RESEARCH PROJECTS
2011 Species richness and community composition of Geometridae (Lepidoptera) along an altitudinal gradient in PNG
2016 Species diversity of plants, insects, mammals, amphibians and birds of Whiteman Range, Papua New Guinea
2016 Effects of regeneration forest on insects, birds and mammals in lowland rainforests of PNG

BIODIVERSITY CONSULTANCY
2017 Butterfly and dragonfly surveys for the PMA3 PNG ExxonMobil biodiversity Survey, Papua New Guinea
2017 Butterflies and odonates of Uro Creek, Kikori Basin, Gulf Province, Papua New Guinea

2016   Dragonfly survey for the Papua LNG Elk Antelope Biodiversity
        Survey, Papua New Guinea
2015   Entomology & overall project management for the ExxonMobil
        Regeneration Monitoring Project, Papua New Guinea

GRANTS
2015 – 2018   UNDP CbFCCRM grant, Principal investigator –
        Biodiversity survey and socio-economic assessment of the
        Whiteman Range, West New Britain Province, PNG, PGK 3000,
        000.00
2015 – 2017   UNDP GEF grant, Principal Investigator -Biodiversity
        value of regenerating forests in Papua New Guinea, PGK
        180,000.00
2009 – 2010   PNG Mamagraun grant, Co-principal investigator - The
        effect of increasing altitude on leaf –hoppers, geometrid moths,
        butterflies and frogs along complete forest transect in Papua New
        Guinea, PGK 48,430.00

AWARDS
2015   Best oral presentation, ATBC – Asian Chapter Conference,
        Cambodia
2008   First Class Honors, University of Papua New Guinea

INTERNATIONAL COURSES
2015   Research Methods and Statistical Analysis Course by Association
        of Tropical Biology & Conservation – Asian Chapter, Cambodia
2012   Tropical Biology Course by the Organization for Tropical Studies
        (OTS) in Costa Rica
2010   Field Biology Course by the Harvard University, the Arnold
        Arboretum and the Center for Tropical Forest Science, Borneo,
        Malaysia
2008   International Tropical Ecology Course by the New Guinea
        Binatang Research Center, PNG Institute of Biological Research
        and the University of South Bohemia, Czech Republic
2007   Biological Research Technique Course by the Wildlife
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2007   Forgarty Summer Intern Course by the PNG Institute of Medical
        Research, Goroka, PNG

PUBLICATIONS

Toko, P. S., B. Koane, K. Molem, S. E. Miller, and V. Novotny. (2023). Ecological trends in moth communities (Geometridae, Lepidoptera) along a complete rainforest elevation gradient in Papua New Guinea. *Insect Conservation and Diversity* 16:649–657.

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Beck, J., McCain, C.M., Axmacher, J.C., Ashton, L.A., Bärtschi, F., Brehm, G., Choi, S.-W.W., Cizek, O., Colwell, R.K., Fiedler, K., Francois, C.L., Highland, S., Holloway, J.D., Intachat, J., Kadlec, T., Kitching, R.L., Maunsell, S.C., Merckx, T., Nakamura, A., Odell, E., Sang, W., **Toko, P.S**., Zamecnik, J., Zou, Y., & Novotny, V. (2017) Elevational species richness gradients in a hyperdiverse insect taxon: a global meta-study on geometrid moths. *Global Ecology and Biogeography*, 26:412-424

Schmiedel, U., Araya, Y., Bortolotto, M. I., Boeckenhoff, L., Hallwachs, W., Janzen, D., Kolipaka, S. S., Novotny, V., Palm, M., Parfondry, M., Smanis, A., & **Toko, P**. (2016). Contributions of paraecologists and parataxonomists to research, conservation, and social development. *Conservation Biology*, 30:506–519. https://doi.org/10.1111/cobi.12661

Novotny, V. and **Toko, P**. (2015). Ecological research in Papua New Guinean rainforests: insects, plants and people. Pp. 71-85 in Bryan, J. E. & Shearman, P. L. (Eds.) *The State of the Forests of Papua New Guinea 2015. Measuring change over period 2002-2014.* University of Papua New Guinea, Port Moresby.

PUBLICATIONS SUMBITTED AND IN PREPARATION

Toko, P. S., Dem, F., Cámara-Leret, R., Martins, D. J., Philip, J., Matapi, U., West, P. & Novotny, V. Biodiversity conservation with Indigenous peoples in the tropics. *Nature*. (Manuscript submitted)

Toko, P. S., Lilip, R., Ibalim, S., Amick, P. K., Miller, S. E. & Novotny, V. (Manuscript) Composition and structure of rainforest moth (Geometridae, Lepidoptera) communities along an island elevational gradient in New Britain (Papua New Guinea). In prep.

CONFERENCES: POSTERS, ORAL PRESENTATIONS

2019 Oral presentation – *Ecological trends of Geometridae at Mt Wilhelm elevational gradient, PNG*. ATBC-AP Conference, Sri Lanka

2019 Oral presentation - *Ecological trends of Geometridae at Mt Wilhelm elevational gradient, PNG*, Czech Ecological Conference, Olomouc, Czech Republic 2013 Oral presentation - *Biodiversity research in PNG*. James Cook University, Cairns, Australia

2015 Oral presentation - *Species richness and community composition of moths (Geometridae) along a complete rainforest gradient in Papua New Guinea*. ATBC Conference, Phnom Penh, Cambodia.

2012 Poster presentation - *Species richness and community composition of moths (Geometridae) along a complete rainforest gradient in Papua New Guinea*, Principia College, Illinois, USA.

2012 Poster presentation - *Species richness and community composition of moths (Geometridae) along a complete rainforest gradient in Papua New Guinea*, Taison Research Center, Saint Louis, USA.

2014 Oral presentation – *Geometridae and drivers of its elevational patterns along a complete rainforest gradient in Papua New Guinea* ATBC Conference, Cairns, Australia

CONSULTANCY REPORTS

Toko, P. S. (2019). Butterflies in S. J. Richards, (editor). Results of the second PMA3 Biodiversity Monitoring Survey of the PNG LNG Upstream Project Area, page 25-39, 10–31 May 2017. ExxonMobil PNG Limited, Port Moresby

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V. Novotny, **P. S. Toko**, J. Moses, P. Szefer, G. Weiblen, K. Molem, B. Bau, C. Alok, E. Tamtiai, F. Philip, J. Auga, K. Pomoh, M.

Rimandai, M. Mogia and M. Manumbor. (2016). PNG ExxonMobil
Regeneration Survey Report. PNG

INTERESTS
Tropical ecology of Lepidoptera and Odonata
Tropical biodiversity conservation

LANGUAGE
English - proficient
Melanesian Tok Pisin - proficient
Native languages: Agarabi (Kainantu) and Fore (Okapa) - proficient

Ecological trends in geometrid moth communities along elevational gradients in tropical rainforests with lessons for tropical biodiversity conservation

Ph.D. Thesis, 2023