SIVAUTL et al.

Species richness and community structure of bats along a forest elevational transect in

Papua New Guinea

Elise Sivault^{1,2*}, Pita K. Amick^{3,4,5}, Kyle N. Armstrong^{6,7}, Vojtech Novotny^{1,2}, Katerina Sam^{1,2}

¹Faculty of Science, University of South Bohemia, Branisovska 1760, 370 05 Ceske Budejovice, Czech Republic, ²Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic, ³Biological Science Division, University of Papua New Guinea, PO Box 320, Papua New Guinea, ⁴The New Guinea Binatang Research Centre, PO Box 604, Madang, Papua New Guinea, ⁵Amick Environmental Consulting, PO Box 1179 Mt Hagen, 511 Western Highlands Province, Papua New Guinea, ⁶ University of Adelaide, North Terrace, Adelaide, South Australia 5005, ⁷ South Australian Museum, North Terrace, Adelaide, South Australia 5000.

*Corresponding author: Elise Sivault, address: Branisovska 31, 370 05 Ceske Budejovice, Czech Republic, email: sivault.e@gmail.com.

Running title: Bat richness and elevation

Received: _____; Revised: _____; Accepted: _____.

SIVAUTL et al.

ABSTRACT

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

Key words: bat communities, species richness, tropical montane, elevational gradient, Papua New Guinea.

SIVAUT et al.

1. INTRODUCTION

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

Among terrestrial vertebrate groups, bats are considered commonly in studies of temperate (Piksa et al., 2013; Scherrer et al., 2019), South American, and African tropical mountain ecosystems (Carvalho et al., 2019; Mongombe et al., 2019; Reardon & Schoeman, 2017). Two predominant patterns of bat species richness have been observed—a decrease with elevation in most tropical regions, and a unimodal trend in temperate regions (McCain, 2007b; McCain & Grytnes, 2010). The area hypothesis states that the amount of land area for each elevational band (e.g., 100–200m) on a mountain will be positively related to the diversity observed in that band (Terborgh, 1973), however, bats showed either no significant relationship or a negative association between species richness and available area (McCain, 2007a). It has

SIVAUT et al.

been suggested that the highest bat species richness occurs in the elevational zone where water and temperature are simultaneously high (i.e., low and mid-elevations in tropical and temperate mountains respectively) (McCain, 2007b). Being small and volant, bats spend much of their energy budget on flight and thermoregulation, which is dependent on ambient temperature and therefore, limits their distribution in cold temperature regimes (Graham, 1983; McNab, 1982). In addition, water availability and temperature indirectly influence food resource availability (e.g., through fruiting tree phenology, the abundance of arthropods), and vegetation (e.g., shrub density), thereby influencing foraging behaviour and the availability of roosting sites (Charbonnier et al., 2016; Moura et al., 2016). While abiotic factors (i.e., temperature, available area within an elevation band) have been explored often in existing models, biotic factors as food resources and habitat characteristics have been considered rarely.

In addition to species richness, the species composition of bat assemblages can vary along an elevational gradient under different scenarios. It has been suggested that high-elevation bat species are able to exist at all elevations because of broad physiological tolerance and ecological requirements (e.g., Stevens, 1992). However, under a scenario of climate change, bat species are acclimated to high mountain conditions because they are geographically, ecologically, and/or physiologically constrained to high elevations (e.g., LaVal, 2004). Thus, species found only at high elevations are likely to expand their ranges or be strictly constrained by recent events of climate change.

Feeding specialization might be another factor affecting assemblage composition. Despite that bat communities are typically dominated by insectivores, the relative species richness of frugivorous and nectarivorous bats peaks in the tropics, especially in the Neotropics, Oceania, and Australasia (Maas et al., 2016). However, patterns in the distribution of bat specialization along elevational gradients have rarely been documented, despite plant and insect distributions

SIVAUULT et al.

varying greatly. Fruiting trees are typically reported to decline in diversity and abundance with increasing elevation (Loiselle & Blake, 1991) while insects follow various patterns (i.e., none, peaking mid-elevation, decreasing, increasing) according to their group and/or localities (Hodkinson, 2005). Consequently, elevation might act as a filter of bat feeding guilds and impact the species composition of bat assemblages.

PNG bats represent seven percent of the world's bat diversity (Bonaccorso, 1998; Mammal Diversity Database, 2021). From a total of 95 native species, PNG has at least 19 endemic bat species (Bonaccorso, 1998). In recent decades, this unique richness attracted new research focused on viruses (Breed et al., 2010; Field et al., 2013), metabolism (McNab & Bonaccorso, 2001), and the home range of single species (Bonaccorso et al., 2002; Winkelmann et al., 2000, 2003). However, there is a lack of knowledge of bat community structure due to limited specific focus within larger mammal studies (Helgen, 2007; Helgen et al., 2011). Much of the effort for bat research in the past two decades has been as part of basic inventory surveys, environmental impact assessments and monitoring for industry (Armstrong et al., 2020; Kale et al., 2018; K.P. Aplin and K.N. Armstrong unpublished reports), university research (Bonaccorso et al., 2002; Robson et al., 2012; Wiantoro, 2020) or else as part of biodiversity assessments for conservation organizations (Armstrong et al., 2015a,b; Armstrong & Aplin, 2011, 2014). While there is no central library of PNG bat echolocation calls, these studies have steadily accumulated knowledge and resources that support both acoustics-based and genetics-based identification, underpin recent species profile revisions in the IUCN Red List, and studies of taxonomic resolution (e.g., Wiantoro, 2020). They also mark a shift towards a primary reliance on acoustics-based detection and identification on field surveys, rather than trapping as was relied upon in the past, though trapping is still the best means of surveying for small species in the Pteropodidae and collecting material to allow robust acoustics-based identification.

SIVALT et al.

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

2. METHODS

2.1 Study area

SIVAUULT et al.

We surveyed bat communities along the elevational transect of Mt. Wilhelm in PNG between 200 m and 3,700 m a.s.l. at eight elevational study sites separated by 500 m elevational increments (i.e., 200 m, 700 m, 1,200 m, 1,700 m, 2,200 m, 2,700 m, 3,200 m, and 3,700 m a.s.l. and ± 60 m for each study site due to the rough terrain). The 30 km long elevational transect, which stretches between 5°44'S, 145°2'E and 5°47'S, 145°03'E, is located along the Bismarck Range's northern slope (Figure 1). Vegetation types used here follow Paijmans (1975), i.e., lowland alluvial forest (<500 m a.s.l.), foothill forest (501–1,500 m a.s.l.), lower montane forest (1,501–3,000 m a.s.l.), and upper montane forest (>3,000 m a.s.l.) (Figure S1.1 in Appendix S1 in supporting information). Mean daily temperature decreases linearly ($r = -0.9$) from 27.4°C at the 200 m a.s.l. to 8.37°C at the timberline (3,700 m a.s.l.) (Table S3.2) (Sam et al., 2019). The average annual precipitation is 3,288 mm (local meteorological station) in the lowlands, rising to 4,400 mm at the forest edge, with a distinct condensation zone between 2,500 and 2,700 m a.s.l. (Sam et al., 2019).

2.2 Mist-netting and acoustic surveys

The bat communities were surveyed by mist-netting and by acoustic surveys, during two independent expeditions conducted in wet (February – April 2015) and dry seasons (June – July 2015).

We used portable ultrasonic bat call detectors (Wildlife Acoustics EM3+ and a Pettersson Elektronik D240X connected to a Roland R-05 Wave/MP3 recorder) to record the calls of echolocating bat species. We surveyed the bats at five points separated by 200 meters at each elevation, visiting each of these points for 15 minutes daily (Table S2.1). The points were located along the point-count track of 16 points (150 m apart) used in the previous study of bird communities (Sam et al., 2019). Surveys were conducted for four days per site from February to

SIVAULT et al.

July 2015 after sunset (6 pm) but were only feasible for two days at 3,200 and 3,700 m. Recordings were analysed by opening each WAV file in Adobe Audition version 22.0 and inspecting the spectrograms for bat echolocation pulses. There were three different sampling rates in the data set: 22.05 kHz, 44.1 kHz, and 256 kHz. The characteristic frequency of echolocation pulses was determined after accounting for the sampling rate and was estimated from the power spectrum. Identification of bat species was undertaken in two steps. First, ‘echolocation call types’ were recognised from the recordings and defined based on a standardised naming scheme that has been used in many published and unpublished surveys across Papua New Guinea and Wallacea in recent years (Armstrong et al., 2020, 2015a, b; Armstrong & Aplin, 2011, 2014; Kale et al., 2018) and second, bat species identifications were attributed to each echolocation call type based on information from these and other surveys (annotated species list in Table S2.2 and illustration of call types in Figure S2.2). This two-step approach, along with the provision of illustrated examples of identified call types, provides transparency that allows for future verification of species identifications, and retrospective correction of species names on the basis of updated information. Nomenclature follows the current IUCN Red List profile for each species (<https://www.iucnredlist.org/>).

We set a total of eight mist-nets (length x height: 15 x 3.5 m) in various habitat types per study site, including understorey ‘flyway’ spaces along human tracks, across creeks, and forest openings. We mist-netted five nights (12 hrs per night) per site in the wet season survey. During the dry season, we revisited elevations from 200 to 2,700 m only, and we operated the mist nets over four nights for five hours daily. Mist-nets were moved to a new spot after every two or three nights. All mist-netted bats were identified to species using field guides by Bonaccorso (1998) and Flannery (1995) as well as (Irwin, 2017; Parnaby, 2009) for *Nyctophilus timoriensis* and *Nyctimene cyclotis* (Figure S2.1). However, morphologically similar *Paranyctimene raptor* and

SIVALT et al.

P. tenax could have been misidentified in the field; they can occur in sympatry, as previously observed by Bergmans (2001).

2.3 Regional data and explanatory variables

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

We used the log₁₀-transformed available land area of elevational belts 200 m wide across the whole New Guinea mainland as a proxy for the land area available for respective study sites (e.g., 100–300 m a.s.l., for the 200 m a.s.l. study site; measured in GIS software ARCGIS 9.3 and ERDAS ER Mapper 6). Indeed, an elevation belt of 200 m seems to perform the best as a proxy of the available land area to explain species richness patterns, according to a recent publication (Sam et al., 2019).

Temperature and humidity were recorded every hour for one year (April 2010–July 2011) using a data logger (Comet R3120) placed in the forest interior of each study site. Mean annual temperature decreased at a constant rate, while mean humidity remained high across the entire transect (83.0%–97.4%) (Table S3.2). Thus, we used only mean daily temperature as a predictor variable.

We used three variables related to habitat (Table S3.2), measured at each point (i.e., 16 points per elevational study site, 128 in total, Sam et al., 2019): (1) Average canopy height (using a laser rangefinder; three measures/point), (2) Shrub density (using a vegetation board (Lilith,

SIVAUULT et al.

2007; MacArthur & MacArthur, 1961), five measures/point, 1–3 m height), and (3) Canopy
openness (5 photos/point analysed with a Gap Light Analyzer; Frazer et al., 2001). These three
factors determine the vegetation structure at each site, which is the basis for the organization of
bat foraging guilds, defining flight spaces for foraging bats, and controlling the availability of
roost sites (Charbonnier et al., 2016; Denzinger & Schnitzler, 2013; López-González et al.,
2012).

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

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

2.4 Statistical analysis

We used incidence data (i.e., presence/absence per sampling night) from the acoustic surveys as it
was not possible to separate the vocalizations of individual bats. Mist-netting data were also
converted to incidence data to facilitate comparison. We recorded the number of nights at a
particular elevation when a given species was present. We used sample-based rarefaction to

SIVAUULT et al.

compare species richness by sampling days at each elevation (in EstimateS 9.1; Colwell, 2013) for both methods. We extrapolated the sampling effort by doubling the number of sampling days. Then, we used non-parametric estimators for incidence data (Jackknife1) to compare with the richness observed along the transect using the software EstimateS 9.1 (Colwell, 2013). Abundances (from mist-netting data) and total species richness (from both methods) were also described for each of the three feeding guilds (frugivore-nectarivore, insectivore, frugivore-nectarivore-insectivore).

We produced heatmaps using the Jaccard dissimilarity index to compare bat species composition between sites using the "Vegan" library (Oksanen et al., 2013) in R software (R Core Team, 2020). The first heatmap was run using incidence data from both mist-netting and acoustic surveys. The second one was produced with regional data (i.e., bats from Central Range and Sepik-Ramu basin). We calculated the mean elevation range for all species observed at each elevation in this study and from regional data, then compared local and regional ranges.

Total species richness was used as the dependent variable in Poisson regressions with combinations of five predictor variables (log-transformed): mean daily temperature, canopy height, shrub density, canopy openness, and land area available within 200 m elevational belts (Table S5.1). Similarly, species richness partitioned into feeding guilds was used as the dependent variable with combinations of six variables: mean temperature, land area, fruiting tree richness, and abundances, or moth species richness and abundances. The small size of our dataset did not allow us to test habitat variables in partitioned richness and to include interactions in our models. We used $\Delta AICc$ and Akaike weights (w_1) to interpret regression results and evaluate models and their fits (Anderson & Burnham, 2002). Frugivore and nectarivore species were assigned to one main feeding guild in our models: frugivore-nectarivore. Frugivore-nectarivore-

SIVAUULT et al.

insectivore species (i.e., *Syconycteris australis*) was included into two guilds —the frugivore-nectarivore and insectivore guilds (i.e., its presence was included in two datasets).

3. RESULTS

3.1 Species richness pattern

By mist-netting, we captured 701 individuals of 12 bat species (Table S2.1). We did not capture any individuals above 2,700 m during the wet season and we were not able to resurvey elevations above 2,700 m during the dry season due to logistical constraints. A total of 11 echolocation call types were recognised from the recordings, each of which can be associated with one or more bat species (Figure S2.2). From these, at least ten bat species in five families were recorded (i.e., confirmed) as being present on the survey (Table S2.1). In total, no less than 22 species were observed in five months along the Mt. Wilhelm transect. This represents about 30 % of the regional species pool according to Bonaccorso (1998). Species richness declined with increasing elevation, regardless of the survey method used or the data sources (Figure 2).

The non-parametric estimator “Jackknife 1” matched the species richness trends, but its estimates were higher than the observed curves (Figure 3c, 3d). Specifically, it predicted significantly higher than observed richness at 700 and 2,700 m in audio data and from 200 m to 2,200m in mist-netting data. The species accumulation curves have not reached the plateau during the acoustic surveys at 700 and 2,700 m and by mist-netting at 700 m (Figure 3a, 3b). We noticed a low plateau at 1,700 m in acoustic data and 1,200m in mist-netting data which matched with the decreases observed at these elevations on the species richness trends (Figure 3c, 3d). On the other hand, the rarefaction curves showed that we quickly reached the highest level of species richness at high elevations (3,200–3,700 m) in both survey methods.

SIVALT et al.

The mist-netting data did not reveal a clear pattern of abundances along the elevational transect (Figure S4.1) while the acoustic data could not be used to estimate abundance. Fruit-feeding bats were the most frequently captured (Figure S4.1) and *Syconycteris australis* dominated the samples (Table S2.1). However, in terms of the number of species, the richness of the frugivores-nectarivores and insectivores declined in a similar pattern along the transect (Figure S4.1).

3.2 Drivers of diversity

We first modelled total species richness with the abiotic and habitat variables, followed by partitioned species richness (i.e., frugivore-nectarivore, insectivore) with the abiotic and food variables. Selected according to AICc, the model with the available land area as a single variable performed better than any other combination (Table S5.1) when it included all species or only insectivores, while temperature as a single variable performed better in frugivore species (Table 1). Despite strong correlations between canopy openness ($R > 0.8$) and height ($R > 0.8$) with area and temperature (Figure S3.1), habitat (Figure S6.1) and any food variable (Figure S6.2 and S6.3) did not significantly improve the model.

3.3 Assemblages of bat communities

The heatmap based on the Mt. Wilhelm data (Figure 4a) showed a rapid turnover of communities along the elevation transect. We found high similarity between pairs of communities at the extreme ends of the transect, between 200 and 700 m and between 3,200 and 3,700 m but also at mid-elevation between 1,200 and 1,700 m. The latter pair of sites shared the only species (i.e., *Miniopterus australis*) found at 3,700 m with a total of two species at 3,200 m. However, using regional data (Figure 4b), the heatmap revealed an increasing turnover of species with increasing elevation. Communities also appeared similar between the closest sites (e.g., 200–700 m; 700–

SIVAUTL et al.

1,200 m) except for the highlands. The elevational distribution of bats ends at 3,200 m in regional data (Table S3.1) so that the highest elevation (3,700 m) could not share any species with other sites.

In the regional data, the mean elevation range length of species is increasing with increasing elevation, meaning that species occurring at one elevation tend to be also found at the lowest ones (Figure 5). The same pattern was observed in our community samples except at 3,200 m where it decreased slightly. It means that one of the species recorded by us (i.e., *Miniopterus tristis*/*Pipistrellus collinus*) at 3,200 m was not detected in the lowlands, despite occurring there in the regional data.

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

4. DISCUSSION

Our study was the first detailed bat survey along a forest transect in PNG and revealed that Mt. Wilhelm hosts at least one-third of the bat species richness expected in that region (Bonaccorso, 1998), representing thus an important diversity hotspot. Bat species richness decreased with increasing elevation and the observed pattern was mainly driven by available land area or mean daily temperature. Species turnover was continuous, with most of the bat species occurring in lowlands and only a limited number reaching the higher elevations. However, while this pattern was predictable based on the regional data, our observations at Mt. Wilhelm showed that some

SIVALT et al.

bats were detected only at high elevations and seemed to be missing in the lower parts of their typical ranges. This pattern might be real or affected by sampling effort issues. Extensive studies are required to clarify this pattern and understand bat community structures in PNG.

4.1 Species richness pattern

PNG is home to a very high number of bat species (95 species) and, with 36 species, boasts the second-highest diversity of Old World fruit bats (i.e., family Pteropodidae) in the world after Indonesia (Aziz et al., 2021). However, it is also one of the most data deficient and poorly-understood countries in terms of how the bat communities are structured with respect to their ecological roles (Aziz et al., 2021). Mt. Wilhelm represents a high diversity of bats with at least 22 species out of the 62 expected in that region. Our data indicate that more species would be revealed by a more intensive survey.

The decreasing species richness with increasing elevation followed the main trend found in tropical mountains documented by McCain (2007). As expected, we confirmed differences between results provided by the two sampling methods employed (Kuenzi & Morrison, 1998; Larsen et al., 2007) whereby most of the species captured in the mist nets were frugivores and nectarivores. Insectivorous bats possess specialized anatomical adaptations that enable echolocation and thus, some species are able to detect and avoid the mist-nets (Francis, 1989; Larsen et al., 2007). This likely explains why only two echolocating bat species were captured in our study, in addition to being detected acoustically (Table S2.1 in Appendix S2). The rarefaction curves showed that acoustic surveys would have to be longer than eight days and coupled with all-night recordings from autonomous recorders in order to yield accurate numbers of species at 700 and 2,700 m. Furthermore, a recent study in the Neotropics revealed that the main centre of activity in bat species is in rainforest canopies (Marques et al., 2016), which has already been

SIVALT et al.

observed for birds in PNG (Chmel et al., 2016). However, since we did not survey bats at the canopy level due to logistical challenges, we potentially missed bats flying above the treetops, perhaps because our equipment could not detect the attenuated echolocation signals, or they were simply less likely to reach our understory mist nets (Kalko & Handley, 2001; Marques et al., 2016). Our result underscored the tendency of insectivorous species to avoid mist-nets and the necessity to employ both acoustic and capture methods in the forest canopy and understory.

In terms of abundance, we captured more frugivore-nectarivore individuals in the lowlands (i.e., 200–700 m) but we did not see significant differences in the capture rate from 1,200 to 2,200 m. This contrasts with studies in South American forests (Carvalho et al., 2019) where frugivores declined greatly above 1000 m. At 3,200 to 3,700 m, the habitats along rivers were mostly open (Figure S1.1 in Appendix S1), which made the captures more difficult. That is perhaps why we did not catch any bats above 2,700 m. However, we have no independent way of assessing catchability in the frugivorous species, in contrast with the insectivorous species for which we can detect them acoustically even though they are not easily captured. Therefore, we were unable to resolve whether frugivore-nectarivore are simply missing above 2,700 m due to environmental filters (e.g., fruit production, temperature) or whether it is the result of apparent mist-netting limitations.

4.2 Drivers of diversity

Despite using a range of factors including some rarely considered for bats (i.e., food availability, habitat), our analysis revealed that available land area and mean daily temperature have the strongest effect on bat species richness along the elevational transect. The area available in the 200 m elevational belt around the study site was the best predictor in the models including all the species or insectivores only, followed closely by temperature in explanatory power. It followed

SIVAUT et al.

the long-known and very robust pattern of the species-area relationship (May, 1975; Rosenzweig, 1995), where the number of species increases with the size of the area.

Temperature was the best predictor of frugivorous species. As such, our data mirror those from other studies conducted in tropical mountains where temperature was also reported to be a strong correlate with bat diversity (McCain, 2007b). Temperature could affect distributions through direct (e.g., physiology) or indirect effects (e.g., habitat, food resources) in different ways between feeding guilds. Mean daily temperatures were 9.9 and 7.9 °C at 3,200 and 3,700 m respectively, which is below the temperature tolerance of most bat species (Appel et al., 2019; Turbill, 2008) and may explain why we did not capture any bats at these sites, and only recorded two species above 2,700 m. Besides, temperature could influence bat species richness indirectly through vegetation and food resources (Charbonnier et al., 2016; Moura et al., 2016). Indeed, vegetation structure could be important for bats, indirectly related to food resources, but also for roosting sites (Capaverde et al., 2018; Kunz, 1982; Perry et al., 2007). Roosting opportunities depend on the number of trees of appropriate size and whether or not they contain cavities or other structures appropriate for bats. Based on published data, 67 % of the species detected in Mt. Wilhelm potentially use foliage or tree hollows (Table S8.1 in Appendix S8). In addition, insect abundance, and fruit and nectar production are all predicted to be low at high elevations (Loiselle & Blake, 1991; Terborgh, 1977). Studies suggest that the reduction in productivity with elevation (McCain & Grytnes, 2010) has a more substantial impact on fruit resources (e.g., figs) than on the other types of resources used by bats (e.g., insects) (Presley et al., 2012; Segar et al., 2017). The distribution of moths from Mt. Wilhelm shows a mid-peak pattern (Beck et al., 2017; Toko, 2011), which does not seem to be followed by insectivorous bats. This is in contrast with patterns in abundances of insectivorous birds of Mt. Wilhelm which peaked in abundance at mid-

SIVALT et al.

elevations, where habitat complexity was the greatest and arthropod abundances were still relatively high (Sam et al., 2020).

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

4.3 Assemblages of bat communities

According to regional data, species turnover kept increasing from similar communities in the lowest study sites (200–700 m) to more dissimilar ones in the highest sites (2,200–3,200 m). Nevertheless, the communities of bats found at the highest sites were just a subset of bats from the lowlands, suggesting that the vast majority of the bat species found in this region are not restricted to mountainous areas. However, potential identification issues and unresolved taxonomy might affect the understanding of species elevational distributions, especially in this long-standing regional dataset (Bonaccorso, 1998).

Our study is the first bat survey conducted at the highest peak of PNG. We detected bats at the 3700 m elevation band—never before recorded in PNG (Amick et al., 2021)—and observed wider bat ranges than the ones described previously for the region (Bonaccorso, 1998). These range extensions are most likely due to low sampling effort for bats at high elevations in PNG in the past, rather than any recent range expansions. In Mt. Wilhelm surveys, we found bat species at high elevations that were missing from the lowlands (*M. tristis*/*P. collinus*, *H. wollastoni*, *O. secundus*), which have been encountered more commonly at mid-high elevations.

SIVAUT et al.

Globally, previous studies showed that the majority of bats found in highlands are primarily lowland species that occasionally commute to higher elevations when conditions become favourable (Alberdi et al., 2015; Michaelsen, 2010) or use these environments as commuting routes. Indeed, as previously mentioned, most bats are limited by direct and/or indirect effects of temperature, and life at high elevations could present an energetic challenge, especially for pregnant and lactating females (Kunz et al., 1995). In our sampling, low canopy openness in the lowlands could affect our ability to detect echolocation signals from bats flying over the canopy. Moreover, changes in call structure at high elevations have already been observed for one bat species (i.e., *Tadarida brasiliensis*) in a previous study (Gillam et al., 2009). Nevertheless, under a scenario of climate change, these bat species (i.e., *M. tristis*/*P. collinus*, *H. wollastoni*, *O. secundus*) may have been recently constrained to high elevations because of spatial elements and/or their ecology and/or physiology. However, we are unable to resolve whether we likely missed these species in the lowlands because of the use of methods that have a greater bias towards the detection of species below the canopy or whether these bat species spanning only in high elevations are the consequences of acclimations to climate change. Extensive surveys with a greater level of effort might help to answer this question.

5. CONCLUSION

Mt. Wilhelm provides habitat for a globally significant bat fauna whose species richness follows the typical decreasing pattern with elevation found in other tropical mountains. Available land area and mean daily temperature explained the vast majority of this pattern, however, we suspect that additional factors (i.e., seasonal food availability) could improve the models. Bat

SIVAULT et al.

438 communities also varied gradually along the elevational transect, as we describe for the first time
 439 for PNG. The fact that six species in this study were recorded above their typical elevational
 440 range (Table S2.1 in Appendix S2), including some detected above the previously described
 441 maximal distribution for PNG, might be the result of climate change or basic survey issues and
 442 lack of good quality historical data. A greater level of effort would shed light on this, which is
 443 potentially important, as the bats of PNG remain largely understudied. This study highlights how
 444 the results of basic inventory surveys that employ a comprehensive, multi-method effort for bat
 445 sampling can be used to address ecological questions that might help with impact assessments.

SIVALT et al.

TABLE LEGENDS

Table 1: Akaike's second-order information criterion (AICc) for single-predictor models of observed bat species richness along the Mt. Wilhelm elevational transect, estimated for all bat observations and the observations partitioned into two feeding guilds. The bold text underlines the model which performed better than any possible combination. Note that only single-predictor models are shown here, while combinations of all the explanatory variables are available in Table S5.1 in Appendix S5.

SIVAUT et al.

TABLE

Table 1.

<i>All bats</i>	$-\log(L)$	Akaike weight (w_i)	AIC_c	ΔAIC_c
Area	14.55	0.458	35.5	0.00
Temperature	15.32	0.212	37	1.54
Canopy height	16.31	0.079	39	3.52
Shrub density	18.79	0.007	44	8.49
Canopy openness	18.85	0.006	44.1	8.61
<i>Frugivores-nectarivores</i>	$-\log(L)$	Akaike weight (w_i)	AIC_c	ΔAIC_c
Temperature	9.31	0.552	25	0.00
Area	9.95	0.289	26.3	1.29
Fruiting tree abundances	15.65	0.001	37.7	12.67
Fruiting tree richness	16.54	0.000	39.5	14.46
<i>Insectivores</i>	$-\log(L)$	Akaike weight (w_i)	AIC_c	ΔAIC_c
Area	13.99	0.482	34.4	0.00
Temperature	14.42	0.312	35.3	0.87
Moth abundances	17.67	0.012	41.7	7.36
Moth richness	17.74	0.011	41.9	7.5

SIVAUULT et al.

FIGURE LEGENDS

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

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

Figure 3: Rarefaction curves of observed and extrapolated (dashed lines) (days x2) number of bat species according to the number of recording (a) or mist-netting days (b) along the elevational transect of Mt. Wilhelm in Papua New Guinea. Observed, estimated (Jackknife1) species richness using audio (c) or mist-nets (d) along elevational transect of the Mt Wilhelm.

Figure 4: Heatmap of Jaccard dissimilarity index of local (mist-netted and acoustic data combined) bat communities found at Mt. Wilhelm (a) and potential bat communities based on the regional distribution of bats in Papua New Guinea (b).

Figure 5: The elevation range for all bat species occurring at each surveyed elevation calculated from Mt. Wilhelm and regional data. Note that only one species is recorded at 3200 m and none at 3700m in the regional data, while we recorded two and one bat species at 3200 and 3700 m respectively (Amick et al., 2021).

SIVAUT et al.

FIGURES

Figure 1.

Figure 2.

SIVAUTL et al.

Figure 3.

Figure 4.

SIVAUTL et al.

Figure 5.

SIVAUT et al.

ACKNOWLEDGMENTS

We thank the landowners of Mt Wilhelm elevational transect and villagers from Bruno Sawmill, Sinopass, Degenumbu, Memeku, Numba, and Kausi for assistance and access to the sites. We also thank P. Toko who shared his database on moth species along Mt Wilhelm elevational transect, and L. Sam and R. Hazel who shared data on the richness of fruiting trees. Binatang Research Centre helped with logistical support and research permits. We acknowledge ERC StG BABE 805189 and GAJU n.04-048/2019/P for financial support. Bat sampling was conducted under research permit 11800056119.

AUTHORS CONTRIBUTIONS

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

DATA AVAILABILITY STATEMENT

The data used for analysis are available in Table S2.1 in Appendix S2 and Tables S3.1, S3.2 in Appendix S3.

SIVAUULT et al.

REFERENCES

- Alberdi, A., Aihartza, J., Aizpurua, O., Salsamendi, E., Brigham, R. M., & Garin, I. (2015).
Living above the treeline: Roosting ecology of the alpine bat *Plecotus macrobullaris*.
European Journal of Wildlife Research, 61(1), 17–25. <https://doi.org/10.1007/s10344-014-0862-8>
- Amick, P. K., Sam, K., Drumo, G., Toko, P. S., & Novotny, V. (2021). Bats can reach 3626 m
a.s.l. in Papua New Guinea: Altitudinal range extensions for six rainforest bat species.
Mammalia. <https://doi.org/10.1515/mammalia-2020-0169>
- Anderson, D. R., & Burnham, K. P. (2002). Avoiding Pitfalls When Using Information-Theoretic
Methods. *The Journal of Wildlife Management*, 66(3), 912–918.
<https://doi.org/10.2307/3803155>
- Appel, G., López-Baucells, A., Magnusson, W. E., & Bobrowiec, P. E. D. (2019). Temperature,
rainfall, and moonlight intensity effects on activity of tropical insectivorous bats. *Journal
of Mammalogy*, 100(6), 1889–1900. <https://doi.org/10.1093/jmammal/gyz140>
- Armstrong, K. N., & Aplin, K. P. (2011). Chapter 19. Bats of the Muller Range, Papua New
Guinea. In S. J. Richard & B. G. Gamui (Eds.), *Rapid Biological Assessments of the
Nakanai Mountains and the upper Strickland Basin: Surveying the biodiversity of Papua
New Guinea's sublime karst environments*. (RAP Bulletin of Biological Assessment 60,
pp. 222–234). Conservation International.
- Armstrong, K. N., & Aplin, K. P. (2014). Chapter 7. A survey of bats (Chiroptera) in the Baiyer
River Wildlife Sanctuary, Western Highlands Province, Papua New Guinea. In S. J.
Richard (Ed.), *A rapid biodiversity assessment of the Baiyer River region, Western
Highlands Province, Papua New Guinea*. (A report to the Mul Baiyer Lumusa District
Administration, pp. 111–113).

SIVAUT et al.

Armstrong, K. N., Aplin, K. P., & Lamaris, J. S. (2015a). Chapter 10. Bats. In S. J. Richard & N. Whitmore (Eds.), *A rapid biodiversity assessment of Papua New Guinea's Hindenburg Wall region*. (pp. 166–180). Wildlife Conservation Society Papua New Guinea Program.

Armstrong, K. N., Mani, A., & Nagombi, E. (2020). Chapter 4. Bats. In S. J. Richards (Ed.), *Results of the third PMA3 Biodiversity Monitoring Survey of the PNG LNG Upstream Project Area, 8 August-2 September 2019*. (pp. 147–181). ExxonMobil PNG Limited.

Armstrong, K. N., Novera, J., & Aplin, K. P. (2015b). Acoustic survey of the echolocating bats of Manus Island and Mussau Island, Papua New Guinea. In N. Whitmore (Ed.), *A Rapid Biodiversity Survey of Papua New Guinea's Manus and Mussau Islands*. (pp. 69–85). Wildlife Conservation Society Papua New Guinea Program.

Aziz, S. A., McConkey, K. R., Tanalgo, K., Sritongchuay, T., Low, M.-R., Yong, J. Y., Mildenstein, T. L., Nuevo-Diego, C. E., Lim, V.-C., & Racey, P. A. (2021). The Critical Importance of Old World Fruit Bats for Healthy Ecosystems and Economies. *Frontiers in Ecology and Evolution*, 9. <https://doi.org/10.3389/fevo.2021.641411>

Beck, J., McCain, C. M., Axmacher, J. C., Ashton, L. A., Bärtschi, F., Brehm, G., Choi, S.-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., ... Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Global Ecology and Biogeography*, 26(4), 412–424. <https://doi.org/10.1111/geb.12548>

Becker, A., Körner, C., Brun, J.-J., Guisan, A., & Tappeiner, U. (2007). Ecological and Land Use Studies Along Elevational Gradients. *Mountain Research and Development*, 27(1), 58–65. [https://doi.org/10.1659/0276-4741\(2007\)27\[58:EALUSA\]2.0.CO;2](https://doi.org/10.1659/0276-4741(2007)27[58:EALUSA]2.0.CO;2)

SIVAUULT et al.

- Bergmans, W. (2001). Notes on distribution and taxonomy of australasian bats. I. Pteropodinae and Nyctimeninae (Mammalia, Megachiroptera, Pteropodidae). *Beaufortia*, 51(8), 119–152.
- Bonaccorso, F. J. (1998). *Bats of Papua New Guinea* (R. A. Mittermeier, W. R. Konstant, & C. G. Burg, Eds.; CI Tropical Field Guide Series). Conservation International.
- Bonaccorso, F. J., Winkelmann, J. R., Dumont, E. R., & Thibault, K. (2002). Home Range of *Dobsonia minor* (Pteropodidae): A Solitary, Foliage-roosting Fruit Bat in Papua New Guinea. *Biotropica*, 34(1), 127–135. <https://doi.org/10.1111/j.1744-7429.2002.tb00248.x>
- Breed, A. C., Yu, M., Barr, J. A., Cramer, G., Thalmann, C. M., & Wang, L.-F. (2010). Prevalence of Henipavirus and Rubulavirus Antibodies in Pteropid Bats, Papua New Guinea. *Emerging Infectious Diseases*, 16(12), 1997–1999. <https://doi.org/10.3201/eid1612.100879>
- Capaverde, U. D., Pereira, L. G. do A., Tavares, V. da C., Magnusson, W. E., Baccaro, F. B., & Bobrowiec, P. E. D. (2018). Subtle changes in elevation shift bat-assemblage structure in Central Amazonia. *Biotropica*, 50(4), 674–683. <https://doi.org/10.1111/btp.12546>
- Carvalho, W. D. de, Martins, M. A., Esbérard, C. E. L., & Palmeirim, J. M. (2019). Traits that allow bats of tropical lowland origin to conquer mountains: Bat assemblages along elevational gradients in the South American Atlantic Forest. *Journal of Biogeography*, 46(2), 316–331. <https://doi.org/10.1111/jbi.13506>
- Cesne, M. L., Wilson, S. W., & Soulier-Perkins, A. (2015). Elevational gradient of Hemiptera (Heteroptera, Auchenorrhyncha) on a tropical mountain in Papua New Guinea. *PeerJ*, 3, e978. <https://doi.org/10.7717/peerj.978>
- Charbonnier, Y. M., Barbaro, L., Barnagaud, J.-Y., Ampoorter, E., Nezan, J., Verheyen, K., & Jactel, H. (2016). Bat and bird diversity along independent gradients of latitude and tree

SIVALT et al.

composition in European forests. *Oecologia*, 182(2), 529–537.
<https://doi.org/10.1007/s00442-016-3671-9>

Chmel, K., Riegert, J., Paul, L., & Novotný, V. (2016). Vertical stratification of an avian community in New Guinean tropical rainforest. *Population Ecology*, 58(4), 535–547.
<https://doi.org/10.1007/s10144-016-0561-2>

Colwell, R. K. (2013). *EstimateS, Version 9.1: Statistical estimation of species richness and shared species from samples*. <http://purl.oclc.org/estimates>

Davis, M. B., & Shaw, R. G. (2001). Range Shifts and Adaptive Responses to Quaternary Climate Change. *Science*, 292(5517), 673–679.
<https://doi.org/10.1126/science.292.5517.673>

Denzinger, A., & Schnitzler, H.-U. (2013). Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviors of microchiropteran bats. *Frontiers in Physiology*, 4.
<https://doi.org/10.3389/fphys.2013.00164>

Field, H., de Jong, C. E., Halpin, K., & Smith, C. S. (2013). Henipaviruses and Fruit Bats, Papua New Guinea. *Emerging Infectious Diseases*, 19(4), 670–671.
<https://doi.org/10.3201/eid1904.111912>

Finnie, S., Sam, K., Leponce, M., Basset, Y., Drew, D., Schutze, M. K., Dahl, C., Damag, M., Dilu, M., Gewa, B., Kaupa, B., Keltim, M., Koane, B., Kua, J., Lilip, R., Mogia, M., Philip, F., Ray, B., Sam, L., ... Novotny, V. (2021). Assemblages of fruit flies (Diptera: Tephritidae) along an elevational gradient in the rainforests of Papua New Guinea. *Insect Conservation and Diversity*, 14(3), 348–355. <https://doi.org/10.1111/icad.12456>

Flannery, T. F. (1995). *Mammals of New Guinea* (The Australian Museum). Robert Brown and Associates.

SIVAUULT et al.

- Francis, C. M. (1989). A Comparison of Mist Nets and Two Designs of Harp Traps for Capturing Bats. *Journal of Mammalogy*, 70(4), 865–870. JSTOR. <https://doi.org/10.2307/1381730>
- Frazer, G. W., Fournier, R. A., Trofymow, J. A., & Hall, R. J. (2001). A comparison of digital and film fisheye photography for analysis of forest canopy structure and gap light transmission. *Agricultural and Forest Meteorology*, 109(4), 249–263. [https://doi.org/10.1016/S0168-1923\(01\)00274-X](https://doi.org/10.1016/S0168-1923(01)00274-X)
- Gillam, E. H., McCracken, G. F., Westbrook, J. K., Lee, Y.-F., Jensen, M. L., & Balsley, B. B. (2009). Bats aloft: Variability in echolocation call structure at high altitudes. *Behavioral Ecology and Sociobiology*, 64(1), 69–79. <https://doi.org/10.1007/s00265-009-0819-1>
- Gradstein, S. R., Homeier, J., & Gansert, D. (Eds.). (2008). *The tropical mountain forest*. Universitätsverlag Göttingen. <https://doi.org/10.17875/gup2008-702>
- Graham, G. L. (1983). Changes in Bat Species Diversity along an Elevational Gradient up the Peruvian Andes. *Journal of Mammalogy*, 64(4), 559–571. <https://doi.org/10.2307/1380511>
- Helgen, K. M. (2007). The mammal fauna of the Kaijende Highlands, Enga Province, Papua New Guinea. In *A Rapid Biodiversity Assessment of the Kaijende Highlands, Enga Province, Papua New Guinea*. Conservation international.
- Helgen, K. M., Opiang, M. D., & Thomas, W. H. (2011). The mammal fauna of Wanakipa, Southern Highlands Province, Papua New Guinea. In *Rapid Assessment Program Bulletin of Biological Assessment* (pp. 246–258). <http://repository.si.edu/xmlui/handle/10088/16737>
- Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, 80(3), 489–513. <https://doi.org/10.1017/S1464793105006767>

SIVAUULT et al.

- Irwin, N. (2017). A new tube-nosed fruit bat from New Guinea, *Nyctimene wrightae* sp. Nov., a re-diagnosis of *N. certans* and *N. cyclotis* (Pteropodidae: Chiroptera), and a review of their conservation status. *Records of the Australian Museum*, 69(69), 73–100.
<https://doi.org/10.3853/j.2201-4349.69.2017.1654>
- Kale, E., Armstrong, K. N., & Amick, P. K. (2018). Chapter 1.6. Mammals of the Wau Creek proposed Wildlife Management Area, Gulf Province, Papua New Guinea, pp. 125-151; Chapter 2.6. Mammals of the Uro Creek catchment, Gulf Province, Papua New Guinea, pp. 245-270; and Chapter 3.6. Mammals of the Lake Kutubu Wildlife Management Area, Southern Highlands Province, Papua New Guinea, pp. 353-378. In S. J. Richards (Ed.), *Rapid biological assessments of Wau Creek, Uro Creek and Lake Kutubu: Documenting biodiversity values to promote forest conservation in the Kikori River Basin, Papua New Guinea*. ExxonMobil PNG Limited.
- Kalko, E. K. V., & Handley, C. O. (2001). Neotropical bats in the canopy: Diversity, community structure, and implications for conservation. In K. E. Linsenmair, A. J. Davis, B. Fiala, & M. R. Speight (Eds.), *Tropical Forest Canopies: Ecology and Management* (Vol. 69, pp. 319–333). Springer Netherlands. https://doi.org/10.1007/978-94-017-3606-0_26
- Kuenzi, A. J., & Morrison, M. L. (1998). Detection of Bats by Mist-Nets and Ultrasonic Sensors. *Wildlife Society Bulletin (1973-2006)*, 26(2), 307–311. JSTOR.
- Kunz, T. H. (1982). Roosting Ecology of Bats. In T. H. Kunz (Ed.), *Ecology of Bats* (pp. 1–55). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_1
- Kunz, T. H., Whitaker, J. O., & Wadanoli, M. D. (1995). Dietary energetics of the insectivorous Mexican free-tailed bat (*Tadarida brasiliensis*) during pregnancy and lactation. *Oecologia*, 101(4), 407–415. <https://doi.org/10.1007/BF00329419>

SIVAUT et al.

- Larsen, R. J., Boegler, K. A., Genoways, H. H., Masfield, W. P., Kirsch, R. A., & Pedersen, S. C. (2007). Mist netting bias, species accumulation curves, and the rediscovery of two bats on Montserrat (Lesser Antilles). *Acta Chiropterologica*, 9(2), 423–435.
[https://doi.org/10.3161/1733-5329\(2007\)9\[423:MNBSAC\]2.0.CO;2](https://doi.org/10.3161/1733-5329(2007)9[423:MNBSAC]2.0.CO;2)
- LaVal, R. K. (2004). Impact of Global Warming and Locally Changing Climate on Tropical Cloud Forest Bats. *Journal of Mammalogy*, 85(2), 237–244.
<https://doi.org/10.1644/BWG-016>
- Lilith, M. (2007). *Do pet cats (Felis catus) have an impact on species richness and abundance of native mammals in low-density Western Australian suburbia?* [Unpublished PhD Dissertation]. Murdoch University.
- Lofthus, Ø., Newman, M. F., Jimbo, T., & Poulsen, A. D. (2020). The Pleuranthodium (Zingiberaceae) of Mount Wilhelm, Papua New Guinea. *Blumea - Biodiversity, Evolution and Biogeography of Plants*, 65(2), 95–101.
<https://doi.org/10.3767/blumea.2020.65.02.01>
- Loiselle, B. A., & Blake, J. G. (1991). Temporal Variation in Birds and Fruits Along an Elevational Gradient in Costa Rica. *Ecology*, 72(1), 180–193.
<https://doi.org/10.2307/1938913>
- López-González, C., Presley, S. J., Lozano, A., Stevens, R. D., & Higgins, C. L. (2012). Metacommunity analysis of Mexican bats: Environmentally mediated structure in an area of high geographic and environmental complexity. *Journal of Biogeography*, 39(1), 177–192. <https://doi.org/10.1111/j.1365-2699.2011.02590.x>
- Maas, B., Karp, D. S., Bumrungsri, S., Darras, K., Gonthier, D., Huang, J. C.-C., Lindell, C. A., Maine, J. J., Mestre, L., Michel, N. L., Morrison, E. B., Perfecto, I., Philpott, S. M., Şekercioğlu, Ç. H., Silva, R. M., Taylor, P. J., Tschardtke, T., Van Bael, S. A., Whelan,

SIVAUULT et al.

673 C. J., & Williams-Guillén, K. (2016). Bird and bat predation services in tropical forests
674 and agroforestry landscapes. *Biological Reviews*, 91(4), 1081–1101.
675 <https://doi.org/10.1111/brv.12211>

676 MacArthur, R. H., & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology*, 42(3), 594–
677 598. <https://doi.org/10.2307/1932254>

678 Mammal Diversity Database. (2021). *Mammal Diversity Database (Version 1.5)*.
679 <https://zenodo.org/record/4139818#.X6Kw6ohKiUk>

680 Marki, P. Z., Sam, K., Koane, B., Kristensen, J. B., Kennedy, J. D., & Jønsson, K. A. (2016).
681 New and noteworthy bird records from the Mt. Wilhelm elevational gradient, Papua New
682 Guinea. *Bulletin of the British Ornithologists' Club*, 136, 263–271.

683 Marques, J. T., Pereira, M. J. R., & Palmeirim, J. M. (2016). Patterns in the use of rainforest
684 vertical space by Neotropical aerial insectivorous bats: All the action is up in the canopy.
685 *Ecography*, 39(5), 476–486. <https://doi.org/10.1111/ecog.01453>

686 May, R. M. (1975). Patterns of species abundance and diversity. *Ecology and Evolution of*
687 *Communities*, 81–120.

688 McCain, C. M. (2005). Elevational Gradients in Diversity of Small Mammals. *Ecology*, 86(2),
689 366–372. <https://doi.org/10.1890/03-3147>

690 McCain, C. M. (2007a). Area and Mammalian Elevational Diversity. *Ecology*, 88(1), 76–86.
691 [https://doi.org/10.1890/0012-9658\(2007\)88\[76:AAMED\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[76:AAMED]2.0.CO;2)

692 McCain, C. M. (2007b). Could temperature and water availability drive elevational species
693 richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16(1),
694 1–13. <https://doi.org/10.1111/j.1466-8238.2006.00263.x>

695 McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and*
696 *Biogeography*, 18(3), 346–360. <https://doi.org/10.1111/j.1466-8238.2008.00443.x>

SIVALT et al.

- McCain, C. M. (2010). Global analysis of reptile elevational diversity. *Global Ecology and Biogeography*, 19(4), 541–553. <https://doi.org/10.1111/j.1466-8238.2010.00528.x>
- McCain, C. M., & Colwell, R. K. (2011). Assessing the threat to montane biodiversity from discordant shifts in temperature and precipitation in a changing climate. *Ecology Letters*, 14(12), 1236–1245. <https://doi.org/10.1111/j.1461-0248.2011.01695.x>
- McCain, C. M., & Grytnes, J.-A. (2010). Elevational Gradients in Species Richness. In *Encyclopedia of Life Sciences (ELS)* (John Wiley&Sons). <https://novel-coronavirus.onlinelibrary.wiley.com/doi/abs/10.1002/9780470015902.a0022548>
- McNab, B. K. (1982). Evolutionary Alternatives in the Physiological Ecology of Bats. In T. H. Kunz (Ed.), *Ecology of Bats* (pp. 151–200). Springer US. https://doi.org/10.1007/978-1-4613-3421-7_4
- McNab, B. K., & Bonaccorso, F. J. (2001). The metabolism of New Guinean pteropodid bats. *Journal of Comparative Physiology B*, 171(3), 201–214. <https://doi.org/10.1007/s003600000163>
- Michaelsen, T. C. (2010). Steep Altitudinal Gradients Can Benefit Lowland Bats. *Folia Zoologica*, 59(3), 203–205. <https://doi.org/10.25225/fozo.v59.i3.a5.2010>
- Mongombe, A. M., Fils, E.-M. B., & Tamesse, J. L. (2019). Diversity and altitudinal distribution of bats (Mammalia: Chiroptera) on Mount Cameroon. *Tropical Zoology*, 32(4), 166–187. <https://doi.org/10.1080/03946975.2019.1680077>
- Moura, M. R., Villalobos, F., Costa, G. C., & Garcia, P. C. A. (2016). Disentangling the Role of Climate, Topography and Vegetation in Species Richness Gradients. *PLoS ONE*, 11(3). <https://doi.org/10.1371/journal.pone.0152468>
- Noroozi, J., Talebi, A., Doostmohammadi, M., Rumpf, S. B., Linder, H. P., & Schneeweiss, G. M. (2018). Hotspots within a global biodiversity hotspot—Areas of endemism are

SIVAUTL et al.

associated with high mountain ranges. *Scientific Reports*, 8(1), 1–10.
<https://doi.org/10.1038/s41598-018-28504-9>

Novotny, V., Miller, S. E., Basset, Y., Cizek, L., Darrow, K., Kaupa, B., Kua, J., & Weiblen, G. D. (2005). An altitudinal comparison of caterpillar (Lepidoptera) assemblages on Ficus trees in Papua New Guinea. *Journal of Biogeography*, 32(8), 1303–1314.
<https://doi.org/10.1111/j.1365-2699.2005.01225.x>

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2013). Package ‘vegan’. *Community Ecology Package*, 2(9), 1–295. CRAN.

Orivel, J., Klimes, P., Novotny, V., & Leponce, M. (2018). Resource use and food preferences in understory ant communities along a complete elevational gradient in Papua New Guinea. *Biotropica*, 50(4), 641–648. <https://doi.org/10.1111/btp.12539>

Paijmans, K. (1975). No. 35 Explanatory Notes to the Vegetation Map of Papua New Guinea. *CSIRO Land Research Surveys*, 1, 1–45. <https://doi.org/10.1071/lrs35>

Parnaby, H. E. (2009). A taxonomic review of Australian Greater Long-eared Bats previously known as *Nyctophilus timoriensis* (Chiroptera: Vespertilionidae) and some associated taxa. *Australian Zoologist*, 35(1), 39–81. <https://doi.org/10.7882/AZ.2009.005>

Perry, R. W., Thill, R. E., & Leslie, D. M. (2007). Selection of roosting habitat by forest bats in a diverse forested landscape. *Forest Ecology and Management*, 238(1), 156–166.
<https://doi.org/10.1016/j.foreco.2006.10.008>

Piksa, K., Nowak, J., Żmihorski, M., & Bogdanowicz, W. (2013). Nonlinear Distribution Pattern of Hibernating Bats in Caves along an Elevational Gradient in Mountain (Carpathians, Southern Poland). *PLOS ONE*, 8(7), e68066.
<https://doi.org/10.1371/journal.pone.0068066>

SIVAUULT et al.

Presley, S. J., Cisneros, L. M., Patterson, B. D., & Willig, M. R. (2012). Vertebrate metacommunity structure along an extensive elevational gradient in the tropics: A comparison of bats, rodents and birds. *Global Ecology and Biogeography*, 21(10), 968–976. <https://doi.org/10.1111/j.1466-8238.2011.00738.x>

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical computing. <https://www.R-project.org/>

Reardon, S., & Schoeman, M. C. (2017). Species richness, functional diversity and assemblage structure of insectivorous bats along an elevational gradient in tropical West Africa. *Acta Chiropterologica*, 19(2), 273–285. <https://doi.org/10.3161/15081109ACC2017.19.2.005>

Ricketts, T. H., Dinerstein, E., Boucher, T., Brooks, T. M., Butchart, S. H. M., Hoffmann, M., Lamoreux, J. F., Morrison, J., Parr, M., Pilgrim, J. D., Rodrigues, A. S. L., Sechrest, W., Wallace, G. E., Berlin, K., Bielby, J., Burgess, N. D., Church, D. R., Cox, N., Knox, D., ... Wikramanayake, E. (2005). Pinpointing and preventing imminent extinctions. *Proceedings of the National Academy of Sciences*, 102(51), 18497–18501. <https://doi.org/10.1073/pnas.0509060102>

Robson, S. K. A., Inkster, T. E., & Krockenberger, A. K. (2012). *Bats of the YUS Conservation Area, Papua New Guinea: Result 5 Task 3.2*. [Report]. James Cook University. <https://researchonline.jcu.edu.au/23089/>

Rosenzweig, M. L. (1995). *Species Diversity in Space and Time*. Cambridge University Press.

Sam, K., Koane, B., Bardos, D. C., Jeppy, S., & Novotny, V. (2019). Species richness of birds along a complete rain forest elevational gradient in the tropics: Habitat complexity and food resources matter. *Journal of Biogeography*, 46(2), 279–290. <https://doi.org/10.1111/jbi.13482>

SIVAUULT et al.

- 768 Sam, K., Koane, B., Jeppy, S., Sykorova, J., & Novotny, V. (2017). Diet of land birds along an
769 elevational gradient in Papua New Guinea. *Scientific Reports*, 7(1), 1–10.
770 <https://doi.org/10.1038/srep44018>
- 771 Sam, K., Koane, B., Sam, L., Mrazova, A., Segar, S., Volf, M., Moos, M., Simek, P., Sisol, M.,
772 & Novotny, V. (2020). Insect herbivory and herbivores of Ficus species along a rain
773 forest elevational gradient in Papua New Guinea. *Biotropica*, 52(2), 263–276.
774 <https://doi.org/10.1111/btp.12741>
- 775 Scherrer, D., Christe, P., & Guisan, A. (2019). Modelling bat distributions and diversity in a
776 mountain landscape using focal predictors in ensemble of small models. *Diversity and*
777 *Distributions*, 25(5), 770–782. <https://doi.org/10.1111/ddi.12893>
- 778 Segar, S. T., Volf, M., Zima Jnr, J., Isua, B., Sisol, M., Sam, L., Sam, K., Souto-Vilarós, D., &
779 Novotny, V. (2017). Speciation in a keystone plant genus is driven by elevation: A case
780 study in New Guinean Ficus. *Journal of Evolutionary Biology*, 30(3), 512–523.
781 <https://doi.org/10.1111/jeb.13020>
- 782 Smith, J. M. B. (1977). Origins and ecology of the tropicalpine flora of Mt Wilhelm, New
783 Guinea. *Biological Journal of the Linnean Society*, 9(2), 87–131.
784 <https://doi.org/10.1111/j.1095-8312.1977.tb00262.x>
- 785 Souto-Vilarós, D., Houadria, M., Michalek, J., Sisol, M., Isua, B., Kuyaiva, T., Weiblen, G. D.,
786 Novotny, V., & Segar, S. T. (2020). Contrasting patterns of fig wasp communities along
787 Mt. Wilhelm, Papua New Guinea. *Biotropica*, 52(2), 323–334.
788 <https://doi.org/10.1111/btp.12763>
- 789 Stevens, G. C. (1992). The Elevational Gradient in Altitudinal Range: An Extension of
790 Rapoport's Latitudinal Rule to Altitude. *The American Naturalist*, 140(6), 893–911.
791 <https://doi.org/10.1086/285447>

SIVAUULT et al.

- Stevens, R. D., Rowe, R. J., & Badgley, C. (2019). Gradients of mammalian biodiversity through space and time. *Journal of Mammalogy*, 100(3), 1069–1086.
<https://doi.org/10.1093/jmammal/gyz024>
- Szczepański, W. T., Vondráček, D., Seidel, M., Wardhaugh, C., & Fikáček, M. (2018). High diversity of Cetiocyon beetles (Coleoptera: Hydrophilidae) along an elevational gradient on Mt. Wilhelm, New Guinea, with new records from the Bird's Head Peninsula. *Arthropod Systematics & Phylogeny*, 76(2), 323–347.
- Terborgh, J. (1973). Chance, Habitat and Dispersal in the Distribution of Birds in the West Indies. *Evolution*, 27(2), 338–349. <https://doi.org/10.2307/2406973>
- Terborgh, J. (1977). Bird Species Diversity on an Andean Elevational Gradient. *Ecology*, 58(5), 1007–1019.
- Toko, P. S. (2011). *Community structure and species composition of geometrid moths (Lepidoptera: Geometridae) along an altitudinal rainforest gradient in Papua New Guinea*. [Unpublished MSc Dissertation].
- Turbill, C. (2008). Winter activity of Australian tree-roosting bats: Influence of temperature and climatic patterns. *Journal of Zoology*, 276(3), 285–290. <https://doi.org/10.1111/j.1469-7998.2008.00487.x>
- Vestjens, W. J. M., & Hall, L. S. (1977). Stomach Contents of Forty-Two Species of Bats From the Australasian Region. *Wildlife Research*, 4(1), 25–35.
<https://doi.org/10.1071/wr9770025>
- Villemant, C., Robillard, T., Legendre, F., & Leponce, M. (Eds.). (2016). *Insects of Mount Wilhelm, Papua New Guinea* (Muséum national d'Histoire naturelle).
- Volf, M., Laitila, J., Kim, J., Sam, L., Sam, K., Isua, B., Sisol, M., Wardhaugh, C., Vejmelka, F., Miller, S., Weiblen, G., Salminen, J.-P., Novotný, V., & Segar, S. (2020). Compound

SIVAULT et al.

Specific Trends of Chemical Defences in Ficus Along an Elevational Gradient Reflect a
Complex Selective Landscape. *Journal of Chemical Ecology*.
<https://doi.org/10.1007/s10886-020-01173-7>

Wiantoro, S. (2020). *Cryptic diversity and rapid radiation of Indo-Australasian bent-winged bats*
(*Miniopterus Bonaparte, 1837*). [PhD Dissertation]. The University of Adelaide.
Retrieved from <https://hdl.handle.net/2440/130098>

Winkelmann, J. R., Bonaccorso, F. J., Goedeke, E. E., & Ballock, L. J. (2003). Home Range and
Territoriality in the Least Blossom Bat, *Macroglossus minimus*, in Papua New Guinea.
Journal of Mammalogy, 84(2), 561–570. [https://doi.org/10.1644/1545-1542\(2003\)084<0561:HRATIT>2.0.CO;2](https://doi.org/10.1644/1545-1542(2003)084<0561:HRATIT>2.0.CO;2)

Winkelmann, J. R., Bonaccorso, F. J., & Strickler, T. L. (2000). Home Range of the Southern
Blossom Bat, *Syconycteris Australis*, in Papua New Guinea. *Journal of Mammalogy*,
81(2), 408–414. [https://doi.org/10.1644/1545-1542\(2000\)081<0408:HROTSB>2.0.CO;2](https://doi.org/10.1644/1545-1542(2000)081<0408:HROTSB>2.0.CO;2)