

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

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

¹Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

²Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic

³Biological Science Division, University of Papua New Guinea, Port Moresby, Papua New Guinea

⁴The New Guinea Binatang Research Centre, Madang, Papua New Guinea

⁵Amick Environmental Consulting, Mt Hagen, Papua New Guinea

⁶University of Adelaide, Adelaide, South Australia, Australia

⁷South Australian Museum, Adelaide, South Australia, Australia

Correspondence

Elise Sivault, Faculty of Science, University of South Bohemia, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic.
Email: sivault.e@gmail.com

Funding information

European Research Council Starting Grant BABE, Grant/Award Number: 805189; Grant Agency of University of South Bohemia, Grant/Award Number: 014/2022/P

Associate Editor: Jennifer Powers

Handling Editor: Kim McConkey

Abstract

Over the past decades, elevational gradients have become a powerful tool with which to understand the underlying cause(s) of biodiversity. The Mt. Wilhelm elevational transect is one such example, having been used to study the birds, insects, and plants of Papua New Guinea (PNG). However, a survey of mammals from this forest elevational transect was lacking. We thus aimed to investigate patterns in the community structure and species richness of bats (Chiroptera) along the transect, link the species to available regional data, and explain the observed patterns by including environmental characteristics. Bat assemblages were surveyed between 200 m and a timberline at 3700 m a.s.l. at eight study sites separated by 500 m in elevation. We conducted mist-netting and acoustic surveys to detect and identify species at each site. Regional data were compiled to compare local with regional diversity. Finally, biotic (i.e., food availability, habitat features) and abiotic (i.e., mean daily temperature) factors were included in our analyses to disentangle the ecological drivers underlying bat diversity. Results revealed that species richness decreases with ascending elevation and was best explained by a corresponding decrease in temperature. We observed both turnover and nestedness of the species composition at regional scale whereas turnover was dominant at local scale. Extensions and shifts of bat elevational ranges were also found in Mt. Wilhelm. Consequently, despite that the study was restricted to one mountain in PNG, it demonstrates how basic inventory surveys can be used to address ecological questions in other similar and undisturbed tropical mountains.

KEYWORDS

bat communities, beta diversity, elevational gradient, species richness, tropical montane

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, studies on assemblages, and especially of patterns of species richness along elevational gradients, have remained popular for many decades (Stevens et al., 2019). Several meta-analyses of terrestrial

vertebrate groups have emerged in recent times that demonstrate varying trends in species diversity according to geographical location, largely because of their significant climatic differences (i.e., temperature and humidity) (e.g., McCain, 2005, 2007b, 2009, 2010).

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

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

Exploring the different dimensions of β -diversity of bat assemblages may also explain the variations in species composition along environmental gradients. β -diversity can be partitioned into two components: turnover (i.e., replacement of some species by others between assemblages) and nestedness (i.e., species gain or loss between assemblages) (Baselga, 2010). If species are responding to environmental dissimilarities, spatial or historical constraints, then a greater turnover of species will be expected for study sites that have larger dissimilarity (Buckley et al., 2010). In contrast, nestedness

may either reflect the quantity of niches available or occupied at the different study sites or be the result of extinctions or colonizations along the gradient (Ulrich et al., 2009). Studies that analyze the variation in the two components of β -diversity of tropical bat assemblages along elevational gradients are still sparse (Patterson et al., 1996; Presley et al., 2012; Turcios-Casco et al., 2021). The available results reveal that both turnover and nestedness of the bat assemblages can be observed along elevational gradient according to the geographical region.

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

Papua New Guinean bats represent 7% of the world's bat diversity (Bonaccorso, 1998; Mammal Diversity Database, 2021). From a total of 95 species, PNG has at least 19 endemic bat species (Bonaccorso, 1998). In recent decades, this unique richness attracted new research focused on viruses (Breed et al., 2010; Field et al., 2013), metabolism (McNab & Bonaccorso, 2001), and the home range of single species (Bonaccorso et al., 2002; Winkelmann et al., 2000, 2003). However, there is a lack of knowledge of bat community structure due to incidental focus within more encompassing mammal studies (Helgen, 2007; Helgen et al., 2011). Much of the effort for bat research in the past two decades has been as part of basic inventory surveys, environmental impact assessments and monitoring for industry (Armstrong et al., 2020; Kale et al., 2018; K. P. Aplin and K. N. Armstrong *unpublished reports*), university research (Bonaccorso et al., 2002; Robson et al., 2012; Wiantoro, 2020) or else as part of biodiversity assessments for conservation organizations (Armstrong & Aplin, 2011, 2014; Armstrong, Aplin, & Lamaris, 2015; Armstrong, Novera, & Aplin, 2015). 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 toward a primary reliance on acoustics-based detection and identification on field surveys, rather than trapping as was relied upon in the past, though trapping is still the best means of surveying for small species in the Pteropodidae and collecting vouchers to corroborate robust acoustics-based identification.

As a part of the Bismarck Range, Mt. Wilhelm is the highest peak in PNG (4509 m a.s.l.) and offers a complete elevational transect in

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

nevertheless, following the current scenario of climate change, we also expected to find species strictly constraint to high elevations.

2 | METHODS

2.1 | Study area

We surveyed bat assemblages along the elevational transect of Mt. Wilhelm in PNG between 200m and 3700 m a.s.l. at eight elevational study sites separated by 500m elevational increments (i.e., 200m, 700m, 1200m, 1700m, 2200m, 2700m, 3200m, and 3700m a.s.l. and ± 60 m for each study site due to the rough terrain). The 30km 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 Pajmans (1975): that is, lowland alluvial forest (<500m a.s.l.), foothill forest (501–1500m a.s.l.), lower montane forest (1501–3000m a.s.l.), and upper montane forest (>3000m a.s.l.) (Figure S1.1 in Appendix S1). Mean daily temperature decreases linearly ($r = -0.9$) from 27.4°C at the 200m a.s.l. to 8.37°C at the timberline (3700m a.s.l.) (Sam et al., 2019). The average annual precipitation is 3288mm (local meteorological station) in the lowlands, rising to 4400mm at the forest edge, with a distinct condensation zone between 2500 and 2700m a.s.l. (Sam et al., 2019). Two seasons are recognized in PNG—a wet season from December to March and a dry season from May to October.

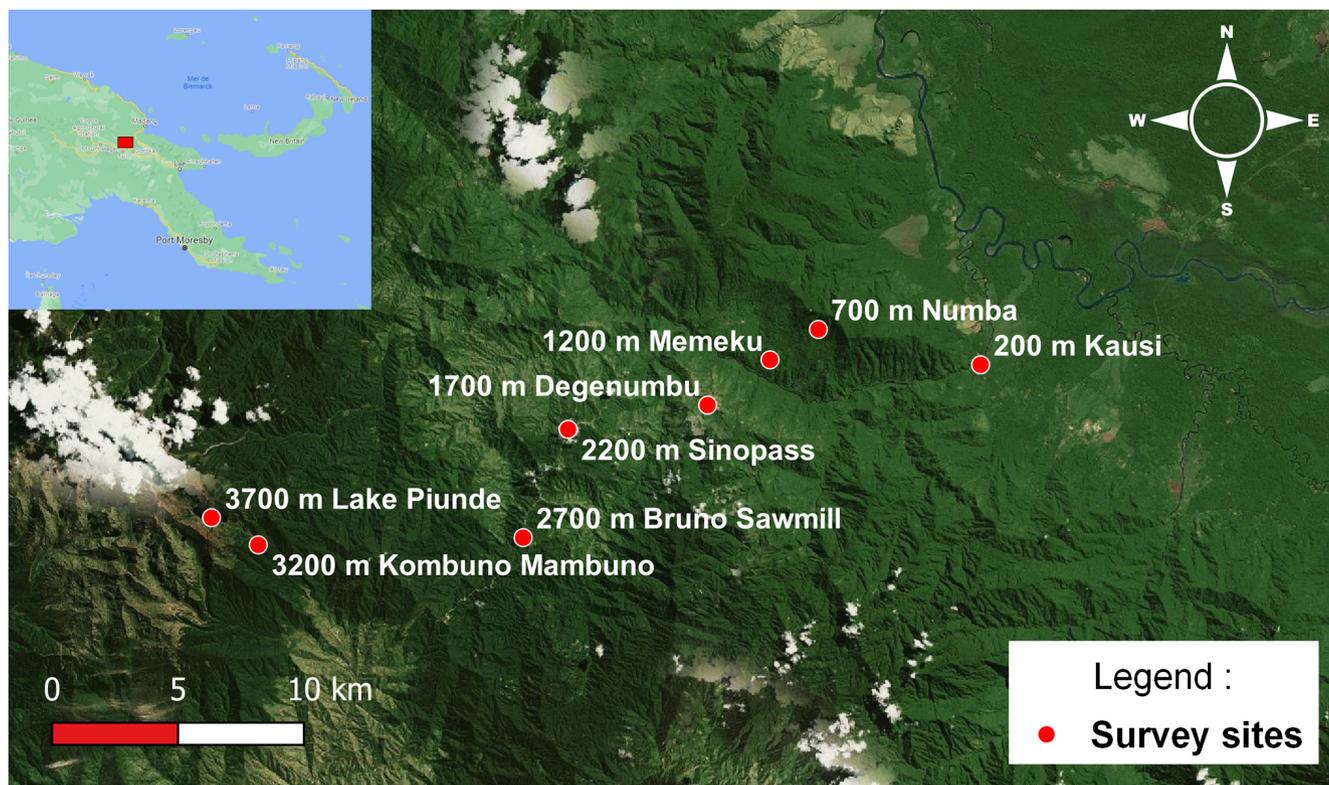


FIGURE 1 Map of the Mt. Wilhelm elevational gradient (source: Google earth; QGIS 3.12.2) and its location in Papua New Guinea (insert with red square).

However, there are only slight seasonal temperature variations in PNG, and therefore, it is generally hot and humid throughout the year (Vincent et al., 2015; Yule, 1996).

2.2 | Mist-netting and acoustic surveys

The bat assemblages were surveyed by mist-netting and by acoustic surveys, during two independent expeditions conducted in wet (February–April 2015) and dry seasons (June–July 2015). We used portable ultrasonic bat call detectors (Wildlife Acoustics EM3+ and a Pettersson Elektronik D240X connected to a Roland R-05 Wave/MP3 recorder) to record the calls of echolocating bat species. At each elevation, we surveyed the bats at five spots separated by 200 meters, visiting each of these spots for 15 min daily along a transect used in the previous study of bird communities (Sam et al., 2019). Surveys were conducted for 4 days per site from February to July 2015 after sunset (6 pm) but were only feasible for 2 days at 3200 and 3700 m a.s.l. (Appendix S1: Table S2.1). Recordings were analyzed 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 recognized from the recordings and defined based on a standardized naming scheme that has been used in many published and unpublished surveys across Papua New Guinea and Wallacea in recent years (Armstrong & Aplin, 2011, 2014; Armstrong, Aplin, & Lamaris, 2015; Armstrong et al., 2020; Armstrong, Novera, & Aplin, 2015; 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 Appendix S1: Table S2.2, distribution of the species in Appendix S1: Table S2.3 and illustration of call types in Appendix S1: Figure S2.1). This two-step approach, along with the provision of illustrated examples of identified call types, provides transparency that allows for future verification of species identifications, and retrospective correction of species names on the basis of updated information. Nomenclature follows the current taxonomic and geographic database of bat species (<https://batnames.org/>).

We set a total of eight mist nets (length \times height: 15 \times 3.5 m) at ground level in various habitat types per study site, including understorey “flyway” spaces along human tracks, across creeks, and forest openings. We mist-netted five nights (12 h per night) per site in the wet season survey. During the dry season, we revisited elevations from 200 to 2700 m a.s.l. only, and we operated the mist nets over four nights for 5 h daily. We were not able to resurvey elevations above 2700 m a.s.l. during the dry season due to logistical constraints. Mist nets were moved to a new spot after every two nights. All mist-netted bats were identified to species using field guides by Bonaccorso (1998) and Flannery (1995) as well as (Irwin, 2017;

Parnaby, 2009) for *Nyctophilus timoriensis* and *Nyctimene cyclotis* (Appendix S1: Figure S2.2). However, morphologically similar *Paranyctimene raptor* and *P. tenax* could have been misidentified in the field; they can occur in sympatry, as previously observed by Bergmans (2001).

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' elevational ranges described in the book (Appendix S1: Table S3.1). The elevational ranges attributed to the bat species came from captures across the whole New Guinea. Nevertheless, it still reflects their tolerance to elevation even though some bat species are not found across the entire PNG area within their elevational range.

Temperature and humidity were recorded every hour for 1 year (April 2010–July 2011) using a data logger (Comet R3120) placed in the forest interior of each study site. We also measured the available land area of elevational belts 200 m wide across the whole New Guinea as a proxy for the land area for respective study sites (e.g., 100–300 m a.s.l., for the 200 m a.s.l. study site; measured in GIS software ARCGIS 9.3 and ERDAS ER Mapper 6). Mean annual temperature and available area decreased at a constant rate with elevation (Appendix S1: Table S3.1), while mean humidity remained high across the entire transect (83.0%–97.4%) (Appendix S1: Table S3.1).

We measured three variables related to habitat (Appendix S1: Table S3.1) at 16 spots per elevational study site (128 in total, Sam et al., 2019): (1) Average canopy height (using a laser rangefinder; three measures/spot), (2) Shrub density (using a vegetation board [Lilith, 2007; MacArthur & MacArthur, 1961], five measures/spot, 1–3 m height), and (3) Canopy openness (5 photographs/spot analyzed with a Gap Light Analyzer; Frazer et al., 2001). These three variables define the vegetation structure at each site, which is the basis for the organization of bat foraging ensembles, defining flight spaces for foraging bats, and controlling the availability of roost sites (Charbonnier et al., 2016; Denzinger & Schnitzler, 2013; López-González et al., 2012).

In addition, we derived several predictors of food availability. Firstly, we used two food variables for frugivorous-nectarivorous bats (Appendix S1: Table S3.1): (1) species richness and (2) abundance of fruiting trees (Villemant et al., 2016). Trees were counted and identified in three random plots of 20 \times 20 m at each study site in the dry season of 2013. Further, we obtained the abundance and richness of the fruiting trees targeted by bats at each elevation by using plant genera recognized as having fruit or nectar consumed by pteropodid bats by the database of Aziz et al. (2021).

Moths (Lepidoptera) dominate the diet of most insectivorous species in PNG (Appendix S1: Table S3.2). We used the (1) species richness and (2) abundance of Geometridae, one of the most important moth families (Beck et al., 2017; Vestjens & Hall, 1977) as an indicator of Lepidoptera availability. The specimens were collected

using manual light trapping (May–August 2009; October–December 2009, January 2010) at all eight study sites of Mt. Wilhelm transect (Beck et al., 2017; Toko, 2011).

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 encountered. Considering that PNG is weakly seasonal, the dry and wet seasons were pooled in all analyses.

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

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

We built a correlation map using the “ggcorrplot” package (Kassambara, 2019) and calculated the significance of the correlations. Elevation, available area, and mean daily temperature were highly correlated ($R = 1$, Appendix S1: Figure S4.1), and the mean humidity was constant along the transect. Thus, we used only the mean daily temperature as an abiotic predictor variable. In addition, we built an index of habitat complexity from the three habitat variables (i.e., canopy height, canopy openness, and shrub density). Indeed, these three factors were highly correlated with each other ($R > 0.8$, except shrub density), and the first axis of a principal component analysis (PCA) summarizing these variables was used as a predictor variable. The first PCA axis accounted for 33% of variation in habitat variables. Similarly, species richness and abundances of moths were highly correlated with each other ($R = 0.9$, Appendix S1: Figure S4.1), and the first axis of a principal component analysis (PCA) summarizing these two variables was used as a predictor variable. The first PCA axis accounted for 41% of variation in the moth variables.

Due to the small size of our dataset, only a limited number of variables could be incorporated into the models. First, we aimed to compare the effect of mean daily temperature and the effect of the habitat structure on bat species richness. Total species richness was used as the dependent variable in Poisson regressions with combinations of two predictor variables (log-transformed): mean daily temperature and the index of habitat complexity. Second, we aimed to compare temperature and food availability on partitioned species richness. Species richness partitioned into feeding guilds was used as the dependent variable with combinations of three variables (log-transformed): mean daily temperature, fruiting tree richness, and abundances, or the index of moth richness and abundance. We used $\Delta AICc$ 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-insectivore species (i.e., *Syconycteris australis*) was included into two guilds—the frugivore-nectarivore and insectivore guilds (i.e., its presence was included in two datasets). To determine the independent contribution of each explanatory variable to the response variable, we applied the hierarchical partitioning algorithm to our datasets using the “hier.part” package (Walsh et al., 2008).

We used Mantel tests to disentangle the effect of mean daily temperature and habitat complexity on the compositional dissimilarity of bat assemblages. Three distance matrices were constructed: (1) a dissimilarity matrix of species composition by elevational study site using the Jaccard coefficient; (2) a Euclidean distance matrix accounting for temperature differences in elevation; and (3) a Euclidean distance matrix accounting for habitat complexity differences in elevation. We performed Mantel tests between bat composition and mean daily temperature, and between bat composition and the index of habitat complexity separately. The Pearson correlation method and 9999 permutations were used by means of the “vegan” package (Oksanen et al., 2013).

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

within elevational sites constant. *P*-values produced by the statistic based on simulations informed us whether the observed turnover and nestedness values were significantly different from those expected by chance.

For screening patterns, elevational ranges of species were ranked by elevational midpoints, minima, maxima, then plotted as bar graphs, producing elevational “range profiles” of the bat species found in Mt. Wilhelm and described in the regional data from (Bonaccorso, 1998).

We used R statistical environment (R Core Team, 2020, version 3.5.2) for all analyses.

3 | RESULTS

3.1 | Species richness pattern

By mist-netting, we captured 701 individuals of 12 bat species (Appendix S1: Table S2.3). We did not capture any individuals above 2700 m.a.s.l. A total of 11 echolocation call types were recognized from the recordings, each of which can be associated with one or more bat species (Appendix S1: Figure S2.1). From these, at least 10 bat species in five families were recorded (i.e., confirmed) as being present on the survey (Appendix S1: Table S2.3). In total, 21 species were observed in 5 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 species accumulation curves did not reach the plateau during the acoustic surveys at 700 and 2700m by mist-netting at

700 m.a.s.l. (Appendix S1: Figure S4.2a, b). On the contrary, the rarefaction curves showed that we quickly reached the highest level of species richness at high elevations (3200–3700 m.a.s.l.) in both survey methods. However, by doubling the sampling days, stability was reached at all elevations, except at 700 m.a.s.l.. Completeness analyses indicated that 92% (ranging from 52 to 100%) of the estimated number of species was collected in average at each site using mist-nets. Using recorder, we, however, detected in average 85% (ranging from 69 to 100%) of the estimated number of species (Appendix S1: Table S2.1).

The mist-netting data revealed that the capture rate was rather constant along the elevational transect (Appendix S1: Figure S5.1) except at 700 m.a.s.l. where it was unusually high. Fruit-feeding bats were the most frequently captured (Appendix S1: Figure S5.2), and *Syconycteris australis* dominated the samples (Appendix S1: Table S2.3). However, in terms of the number of species, the richness of the frugivores-nectarivores and insectivores declined in a similar pattern along the transect (Appendix S1: Figure S5.2).

3.2 | Drivers of diversity

We first modeled total species richness with the mean daily temperature and an index of habitat complexity, followed by partitioned species richness (i.e., frugivore-nectarivore, insectivore) with the mean daily temperature and food variables. Selected according to AICc, the model with the mean daily temperature as a single variable performed better than any other combination (Table 1) regardless of the type of species richness. The hierarchical partitioning analysis showed that the independent effect of the habitat index closely followed the mean daily temperature

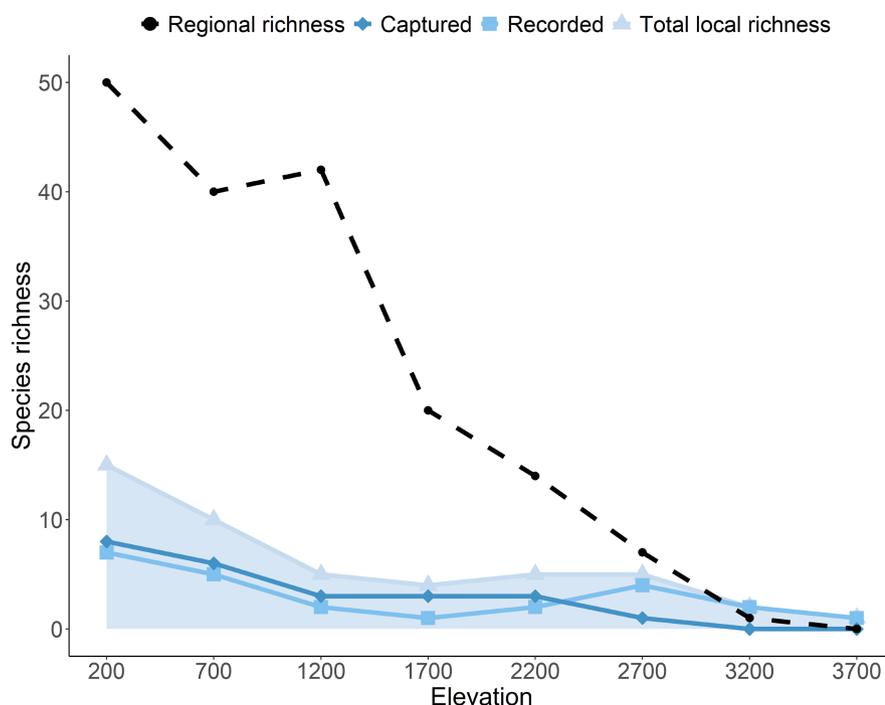


FIGURE 2 Bat species richness recorded from mist-netting captures, acoustic records, and both methods combined, at eight study sites of Mt. Wilhelm elevational transect in Papua New Guinea. Regional species richness according to Bonaccorso (1998).

TABLE 1 Akaike's second-order information criterion (AIC_c) for multi-predictor models of observed bat species richness along the Mt. Wilhelm elevational transect, estimated for all bat observations and the observations partitioned into two feeding guilds.

	-Log(L)	Akaike weight (w_1)	AIC _c	ΔAIC _c
All bats				
Null	25.01	0.000	52.7	15.65
Temperature	15.32	0.679	37.0	0.00
Vegetation index	16.21	0.278	38.8	1.79
Temperature + Vegetation index	15.27	0.043	42.6	5.51
Frugivores-nectarivores				
Null	17.446	0.002	37.6	12.53
Temperature	9.31	0.884	25.0	0.00
Fruiting tree abundances	15.65	0.002	37.7	12.67
Fruiting tree richness	16.54	0.001	39.5	14.46
Temperature + Fruit. tree ab.	9.28	0.055	30.6	5.55
Temperature + Fruit. tree rich.	9.30	0.054	30.6	5.58
Fruit. tree ab. + Fruit. tree rich.	12.51	0.002	37.0	12
Temp. + Fruit. tree rich. + ab.	9.21	0.001	39.8	14.74
Insectivores				
Null	18.37	0.100	39.4	4.16
Temperature	14.42	0.802	35.3	0.00
Moth index	17.67	0.031	41.8	6.50
Temperature + Moth index	14.11	0.067	40.2	4.97

Note: The bold text underlines the model which performed better than any possible combination.

(45% and 55%, respectively) and confirmed that none of the food variables (i.e., fruiting trees and moths) significantly improved the model (Appendix S1: Figure S6.1).

Mantel tests between bat composition and temperature, and between bat composition and the habitat index are both statistically significant (Mantel r : 0.68, p -value = .001, and Mantel r : 0.63, p -value = .007, respectively).

3.3 | Assemblages of bats

The heatmap based on the Mt. Wilhelm data (Figure 3a) showed a rapid turnover of species along the elevation transect. We found high similarity between adjacent assemblages at the extreme ends of the transect, between 200 and 700m and between 3200 and 3700m but also at mid-elevation between 1200 and 1700m a.s.l. The latter pair of sites shared the only species (i.e., *Miniopterus australis*) found at 3700m with a total of two species at 3200m a.s.l. The cluster analysis identified a pronounced distinctiveness of low- to high-elevation bat assemblages (200–2700m a.s.l.) from the highest ones (3200–3700m a.s.l.) (Figure 3c). However, using regional data (Figure 3b), the heatmap revealed an increasing dissimilarity with increasing elevation. Assemblages also appeared similar between the closest sites (e.g., 200–700m; 700–1200m a.s.l.) except for the highlands. The elevational distribution of bats ends at 3200m a.s.l. in regional data (Appendix S1: Figure S3.1) so that the highest elevation

(3700m a.s.l.) could not share any species with other sites. The cluster analysis revealed that the bat assemblages formed two clusters: one between 200m and 1200m and a second one from 1700m to 3700m a.s.l. (Figure 3d).

The complete multiple-site dissimilarity in species composition along the studied elevational transect was high (88%) and dominated by the turnover component (71%), whereas the value of the nestedness-related component was low (17%) (Table 2). However, using regional data, the complete multiple-site dissimilarity in species composition was high (86%) being almost equally driven by the turnover component (46%) and the nestedness-related component (40%) (Table 2).

Profiles of elevational ranges for bats in Mt. Wilhelm are dominated by the large number of species occurring in lowland habitats (76%) (Figure 4a). However, several species are found on the high montane slopes (above 2200m a.s.l.) that do not also occur in the lowlands. Similarly, using regional data, most bat species occur in the lowlands (88% below 700), but several species found at mid-elevations (9%) present evidence of discrete elevational zonation (Figure 4b).

Our results confirmed the upper elevation reported in the literature for most of the species at Mt. Wilhelm, apart from six species: *Hipposideros wollastoni*, *H. calcaratus*, *Dobsonia minor*, *Nyctimene draconilla*, *Paranyctimene raptor*, *Miniopterus australis* [= *Miniopterus* sp. 2 "small"], that were observed at higher elevations (Appendix S1: Figure S7.1).

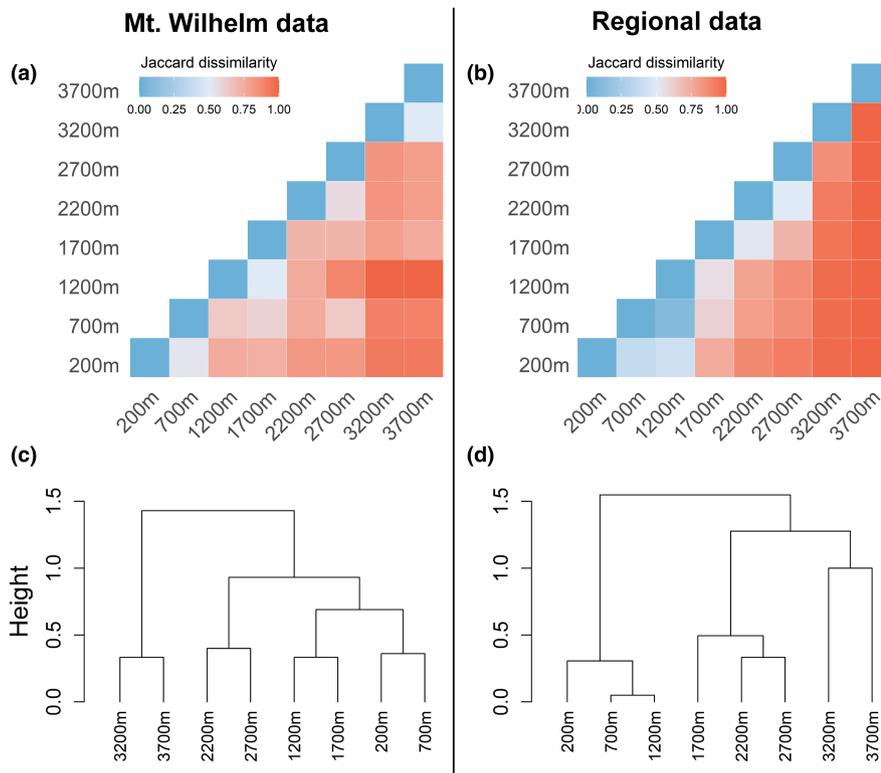


FIGURE 3 Heatmap of Jaccard dissimilarity index of local (mist-netted and acoustic data combined) bat assemblages found at Mt. Wilhelm (a) and potential bat assemblages based on the regional distribution of bats in Papua New Guinea (b). Dendrograms of the dissimilarity for the Mt. Wilhelm bat species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

	Obs (%)	Mean (sim)	2.5%	50%	97.5%	p(sim)
Species by site (Mt. Wilhelm data)						
Turnover	0.71	0.86	0.82	0.86	0.88	<<.001
Nestedness	0.17	0.03	0.01	0.03	0.06	<<.001
Species by site (Regional data)						
Turnover	0.46	0.87	0.85	0.87	0.88	<<.001
Nestedness	0.40	0.01	0.007	0.01	0.02	<<.001

TABLE 2 Null model results of the multiple-site β -diversity components for species by site using the Mt. Wilhelm or the regional data.

Note: β -diversity components are represented by percentage (%) of total dissimilarity. Obs. (%)—percentage represented by β -diversity components of the total dissimilarity; Mean(sim)—mean values of the 9999 simulations; 2.5%, 50% and 97.5%—the number of simulated values; p(sim)—p values.

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

4.1 | Species richness pattern

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

The decreasing species richness with increasing elevation followed the main decreasing pattern found in tropical mountains documented by McCain (2007a, 2007b). Even though the sampling completeness was relatively high regardless of the sampling method

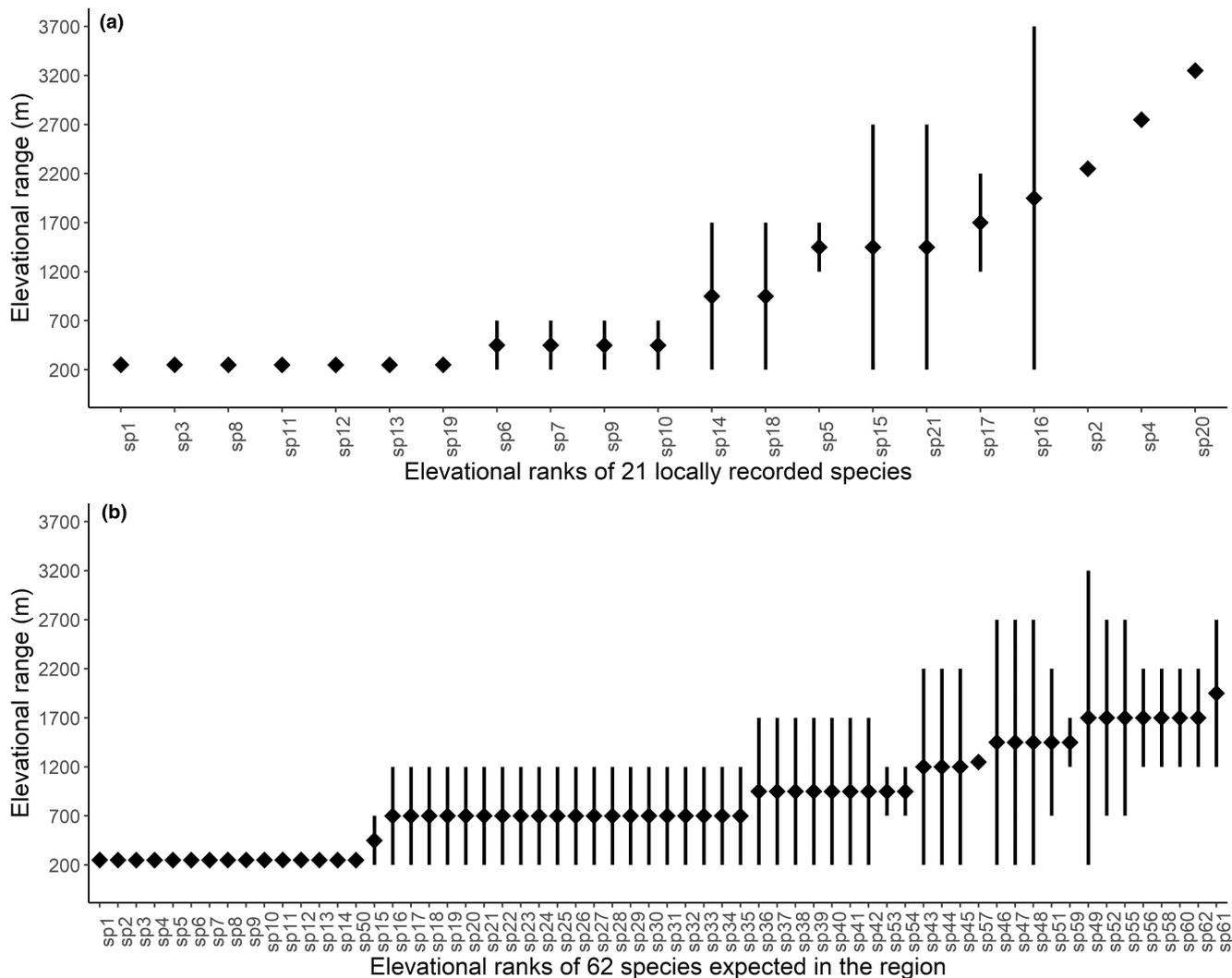


FIGURE 4 Elevational range profiles for the Mt. Wilhelm (a) and the regional dataset (b). Bars indicate the maximum and minimum elevational limits of each species' range, and species are ordered along the abscissa by ranked elevational midpoints.

or the study site, the rarefaction curves showed that acoustic surveys would have to exceed 8 days and coupled with all-night recordings from autonomous recorders to yield accurate numbers of species at 700 and 2700 m a.s.l. Furthermore, a recent study in the Neotropics revealed that the main center of activity in bat species is in rainforest canopies (Marques et al., 2016), which has already been observed for birds in PNG (Chmel et al., 2016). However, since we did not survey bats at the canopy level due to logistical challenges, we potentially missed bats flying above the treetops, perhaps because our equipment could not detect the attenuated echolocation signals, or they were simply less likely to reach our understory mist nets (Kalko & Handley, 2001; Marques et al., 2016). Our result underscored the necessity to employ both acoustic and capture methods in the forest canopy and understory.

In terms of captures, we collected more frugivore-nectarivore individuals in the lowlands (i.e., 200–700 m a.s.l.) but we did not see significant differences in the capture rate from 1200 to 2700 m a.s.l. This contrasts with studies in South American forests (De Carvalho

et al., 2019) where frugivores declined greatly above 1000 m a.s.l. At 3200 to 3700 m a.s.l., the habitats along rivers were mostly open (Figure S1.1 in Appendix S1), which made the captures more difficult, and our sampling effort was the lowest at those elevations. That is perhaps why we did not catch any bats above 2700 m a.s.l. However, we have no independent way of assessing catchability in the frugivorous species, in contrast with the insectivorous species for which we can detect them acoustically even though they are not easily captured. Therefore, we were unable to resolve whether frugivore-nectarivore are simply missing above 2700 m a.s.l. 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 (e.g., food availability), our analysis revealed that mean daily

temperature has the strongest independent effect on bat species richness along the elevational transect, followed closely by the habitat index in explanatory power. Similar results were also revealed by the mantel test, showing that both temperature and habitat were driving the compositional dissimilarity of bat assemblages. As such, our data mirror those from other studies conducted in tropical mountains where temperature was also reported to be a strong correlate with bat diversity (McCain, 2007b) and species composition (Presley et al., 2012). Temperature could affect distributions through direct (e.g., physiology) or indirect effects (e.g., habitat, food resources) in different ways between feeding guilds. Mean daily temperatures were 9.9 and 7.9°C at 3200 and 3700 m a.s.l., respectively, which is below the temperature tolerance of most bat species (Geiser & Stawski, 2011) and may explain why we did not capture any bats at these sites, and only recorded two species above 2700 m a.s.l. Besides, temperature could influence bat species richness indirectly through vegetation and food resources (Charbonnier et al., 2016; Moura et al., 2016). Indeed, the habitat complexity index (combining features of the vegetation structure) had also a strong independent effect on species richness. Vegetation structure could be important for bats, indirectly related to food resources, but also for roosting sites (Capaverde et al., 2018; Kunz, 1982; Perry et al., 2007). Roosting opportunities depend on the number of trees of appropriate size and whether or not they contain cavities or other structures appropriate for bats. Based on published data, 67% of the species detected in Mt. Wilhelm potentially use foliage or tree hollows (Appendix S1: Table S3.2). In contrast, the food variables had a very low effect on species richness of insectivores or frugivores-nectarivores. Insect abundance, and fruit and nectar production are all predicted to be low at high elevations (Loiselle & Blake, 1991; Terborgh, 1977). Studies suggest that the reduction in productivity with elevation (McCain & Grytnes, 2010) has a more substantial impact on fruit resources (e.g., figs) than on the other types of resources used by bats (e.g., insects) (Presley et al., 2012; Segar et al., 2017). The distribution of moths from Mt. Wilhelm shows a mid-peak pattern (Beck et al., 2017; Toko, 2011), which does not seem to be followed by insectivorous bats.

The inclusion of habitat features, fruiting tree and moth species richness, and abundances in the model did not change the relative level of influence of temperature on species richness. However, temperature, decrease linearly with increasing elevation while bat diversity does not. The steepest drop-off in numbers was between 200 m and 1200 m a.s.l. and declining at a slower rate thereafter. It is thus likely that there are also other factors, that we did not consider (e.g., seasonal food availability), modifying the response by bats.

4.3 | Assemblages of bats

According to regional data, dissimilarity kept increasing from similar assemblages in the lowest study sites (200–1200 m a.s.l.) to more dissimilar ones in the highest sites (1700–3200 m a.s.l.) with a clear disconnection of the assemblages between 1200 and 1700 m a.s.l.

The values of turnover and nestedness-related components of dissimilarity showed that both contributed to the distribution pattern of the bat species along the transect. Indeed, the assemblages of bats found at the highest sites were just a subset of bats from the lowlands, suggesting that the vast majority of the bat species found in this region are not restricted to mountainous areas. While some species at intermediate elevations were missing in low elevations and thus increased dissimilarity of the assemblages. However, potential identification issues and unresolved taxonomy might affect the understanding of species elevational distributions, especially in this long-standing regional dataset (Bonaccorso, 1998).

When the scale of the analysis was reduced, we found that species turnover had a large effect in determining beta diversity dissimilarity along the elevational transect of Mt. Wilhelm. Our study is the first bat survey conducted at the highest peak of PNG. We detected bats at the 3700 m a.s.l. elevation band—never before recorded in PNG (Amick et al., 2021)—and observed wider bat ranges than the ones described previously for the region (Bonaccorso, 1998). These range extensions are most likely due to low sampling effort for bats at high elevations in PNG in the past, rather than any recent range expansions. In Mt. Wilhelm surveys, we found bat species at high elevations that were missing from the lowlands (*M. tristis*/*P. collinus*, *H. wollastoni*, *O. secundus*), which have been encountered more commonly at mid-high elevations. Globally, previous studies showed that the majority of bats found in highlands are primarily lowland species that occasionally commute to higher elevations when conditions become favorable (Patterson et al., 1996) or use these environments as commuting routes. Indeed, as previously mentioned, most bats are limited by direct and/or indirect effects of temperature, and life at high elevations could present an energetic challenge, especially for pregnant and lactating females (Kunz et al., 1995). In our sampling, low canopy openness in the lowlands could affect our ability to detect echolocation signals from bats flying over the canopy. Moreover, changes in call structure at high elevations have already been observed for one bat species (i.e., *Tadarida brasiliensis*) in a previous study (Gillam et al., 2009). Nevertheless, under a scenario of climate change, these bat species (i.e., *M. tristis*/*P. collinus*, *H. wollastoni*, *O. secundus*) may have been recently constrained to high elevations because of spatial elements and/or their ecology and/or physiology. However, we are unable to resolve whether we likely missed these species in the lowlands because of the use of methods that have a greater bias toward 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. Mean daily temperature explained the vast majority of this pattern; however, we suspect

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

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.

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 European Research Council Starting Grant BABE 805189 (under Horizon 2020) and Grant Agency of University of South Bohemia n.014/2022/P for financial support. Bat sampling was conducted under research permit 11800056119. Finally, we would like to thank the reviewers for valuable comments and suggestions, which helped us to improve the quality of the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.ns1rn8pww> (Sivault et al., 2022).

ORCID

Elise Sivault  <https://orcid.org/0000-0001-8970-1804>

Katerina Sam  <https://orcid.org/0000-0002-3436-0579>

REFERENCES

- 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*, 86, 150–155. <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>
- 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). Wildlife Conservation Society.
- Armstrong, K. N., Aplin, K. P., & Lamarin, J. S. (2015). 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. (2015). 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., Sritongchuy, 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, 641411. <https://doi.org/10.3389/fevo.2021.641411>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3(5), 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- 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.
- Bergmans, W. (2001). Notes on distribution and taxonomy of australasian bats. I. Pteropodinae and Nyctimeninae (Mammalia, Megachiroptera, Pteropodidae). *Beaufortia*, 51(8), 119–152.
- Bogoni, J. A., Carvalho-Rocha, V., Ferraz, K. M. P. M. B., & Peres, C. A. (2021). Interacting elevational and latitudinal gradients determine bat diversity and distribution across the Neotropics. *Journal of Animal Ecology*, 90(12), 2729–2743. <https://doi.org/10.1111/1365-2656.13594>
- Bonaccorso, F. J. (1998). CI tropical field guide series. In R. A. Mittermeier, W. R. Konstant, & C. G. Burg (Eds.), *Bats of Papua New Guinea*. 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>

- Buckley, L. B., Davies, T. J., Ackerly, D. D., Kraft, N. J. B., Harrison, S. P., Anacker, B. L., Cornell, H. V., Damschen, E. I., Grytnes, J.-A., Hawkins, B. A., McCain, C. M., Stephens, P. R., & Wiens, J. J. (2010). Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, 277(1691), 2131–2138. <https://doi.org/10.1098/rspb.2010.0179>
- Capaverde, U. D., Pereira, L. G., Do, A., Tavares, V. D. 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>
- 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 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>
- De Carvalho, W. D., 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>
- 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, 164. <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.
- 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)
- Geiser, F., & Stawski, C. (2011). Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integrative and Comparative Biology*, 51(3), 337–348. <https://doi.org/10.1093/icb/acr042>
- 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.
- 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. *Rapid Assessment Program Bulletin of Biological Assessment*, 60, 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>
- 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. https://doi.org/10.1007/978-94-017-3606-0_26
- Kassambara, A. (2019). *ggcorrplot: Visualization of a Correlation Matrix using ggplot2*. R Package Version 0.1, 3.
- 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>
- 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 thesis]. 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., Tschamtké, T., Van Bael, S. A., Whelan, C. J., & Williams-Guillén, K. (2016). Bird and bat predation services in tropical forests

- and agroforestry landscapes. *Biological Reviews*, 91(4), 1081–1101. <https://doi.org/10.1111/brv.12211>
- MacArthur, R. H., & MacArthur, J. W. (1961). On Bird Species Diversity. *Ecology*, 42(3), 594–598. <https://doi.org/10.2307/1932254>
- Mammal Diversity Database. (2021). Mammal Diversity Database (Version 1.5). <https://zenodo.org/record/4139818#X6Kw6ohKiUk>
- Marki, P. Z., Sam, K., Koane, B., Kristensen, J. B., Kennedy, J. D., & Jønsson, K. A. (2016). New and noteworthy bird records from the Mt. Wilhelm elevational gradient, Papua New Guinea. *Bulletin of the British Ornithologists' Club*, 136, 263–271.
- Marques, J. T., Pereira, M. J. R., & Palmeirim, J. M. (2016). Patterns in the use of rainforest vertical space by Neotropical aerial insectivorous bats: All the action is up in the canopy. *Ecography*, 39(5), 476–486. <https://doi.org/10.1111/ecog.01453>
- McCain, C. M. (2005). Elevational Gradients in Diversity of Small Mammals. *Ecology*, 86(2), 366–372. <https://doi.org/10.1890/03-3147>
- McCain, C. M. (2007a). Area and Mammalian Elevational Diversity. *Ecology*, 88(1), 76–86.
- McCain, C. M. (2007b). Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16(1), 1–13. <https://doi.org/10.1111/j.1466-8238.2006.00263.x>
- McCain, C. M. (2009). Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, 18(3), 346–360. <https://doi.org/10.1111/j.1466-8238.2008.00443.x>
- 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.
- 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.
- 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>
- 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), e0152468. <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 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.
- 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>
- Pajmans, 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>
- Patterson, B. D., Pacheco, V., & Solari, S. (1996). Distribution of bats along an elevational gradient in the Andes of south-eastern Peru. *Journal of Zoology*, 240(4), 637–658. <https://doi.org/10.1111/j.1469-7998.1996.tb05313.x>
- 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>
- 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/>
- 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>
- Sam, K., Koane, B., Jeppy, S., Sykorova, J., & Novotny, V. (2017). Diet of land birds along an elevational gradient in Papua New Guinea. *Scientific Reports*, 7(1), 1–10. <https://doi.org/10.1038/srep44018>
- Scherrer, D., Christe, P., & Guisan, A. (2019). Modelling bat distributions and diversity in a mountain landscape using focal predictors in ensemble of small models. *Diversity and Distributions*, 25(5), 770–782. <https://doi.org/10.1111/ddi.12893>
- Segar, S. T., Volf, M., Zima Jnr, J., Isua, B., Sisol, M., Sam, L., Sam, K., Souto-Vilarós, D., & Novotny, V. (2017). Speciation in a keystone plant genus is driven by elevation: A case study in New Guinean Ficus. *Journal of Evolutionary Biology*, 30(3), 512–523. <https://doi.org/10.1111/jeb.13020>
- Sivault, E., Amick, P. K., Armstrong, K. N., Novotny, V., & Sam, K. (2022). Data from: Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.ns1rn8pww>
- Smith, J. M. B. (1977). Origins and ecology of the tropicalpine flora of Mt Wilhelm, New Guinea. *Biological Journal of the Linnean Society*, 9(2), 87–131. <https://doi.org/10.1111/j.1095-8312.1977.tb00262.x>
- Souto-Vilarós, D., Houadria, M., Michalek, J., Sisol, M., Isua, B., Kuyaiva, T., Weiblen, G. D., Novotny, V., & Segar, S. T. (2020). Contrasting

- patterns of fig wasp communities along Mt. Wilhelm, Papua New Guinea. *Biotropica*, 52(2), 323–334. <https://doi.org/10.1111/btp.12763>
- 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 Master Thesis) [Master of Science thesis]. University of Papua New Guinea.
- Turcios-Casco, M. A., Gatti, R. C., Dri, G. F., Cáceres, N., Stevens, R., & de Sales Dambros, C. (2021). Ecological gradients explain variation of phyllostomid bat (Chiroptera: Phyllostomidae) diversity in Honduras. *Mammalian Biology*, 101(6), 949–961. <https://doi.org/10.1007/s42991-021-00152-z>
- Ulrich, W., Almeida-Neto, M., & Gotelli, N. J. (2009). A consumer's guide to nestedness analysis. *Oikos*, 118(1), 3–17. <https://doi.org/10.1111/j.1600-0706.2008.17053.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. (2016). *Insects of Mount Wilhelm, Papua New Guinea*. Muséum national d'Histoire naturelle.
- Vincent, J. B., Henning, B., Saulei, S., Sosanika, G., & Weiblen, G. D. (2015). Forest carbon in lowland Papua New Guinea: Local variation and the importance of small trees. *Austral Ecology*, 40(2), 151–159. <https://doi.org/10.1111/aec.12187>
- 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 specific trends of chemical defences in ficus along an elevational gradient reflect a complex selective landscape. *Journal of Chemical Ecology*, 46, 442–454. <https://doi.org/10.1007/s10886-020-01173-7>
- Walsh, C., Mac Nally, R., & Walsh, M. (2008). *The hier. part package. Hierarchical partitioning*. R Project For Statistical Computing.
- Wiantoro, S. (2020). *Cryptic diversity and rapid radiation of Indo-Australasian bent-winged bats (Miniopterus Bonaparte, 1837)*. [PhD thesis]. The University of Adelaide.
- 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.
- 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.
- Yule, C. M. (1996). The ecology of an aseasonal tropical river on Bougainville Island, Papua New Guinea. In F. Schiemer & K. T. Boland (Eds.), *Perspectives in Tropical limnology* (pp. 239–254). SPB Academic Publishing.

SUPPORTING INFORMATION

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

How to cite this article: Sivault, E., Amick, P. K., Armstrong, K. N., Novotny, V., & Sam, K. (2022). Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. *Biotropica*, 00, 1–14. <https://doi.org/10.1111/btp.13161>