

## RESEARCH PAPER

# Species richness of birds along a complete rain forest elevational gradient in the tropics: Habitat complexity and food resources matter

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## Abstract

**Aim:** We examined whether the available surface area, temperature, or habitat complexity (foliage height diversity index) determine species richness of birds (and species richness of individual feeding guilds) along a complete forest elevational gradient. Further, we focused on the relationship between species richness of insectivorous birds and the availability of their food resources.

**Location:** Elevational gradient (200–3,700 m) of Mt Wilhelm (4,509 m a.s.l.), Central Range, Papua New Guinea.

**Taxon:** Birds.

**Methods:** We collected data on bird communities at eight sites (500 m elevational increment) during three surveys encompassing both dry and wet seasons over a 2-year period. We used point counts, mist-netting, and random walks throughout a standardized area. We tested three predictors of diversity and all of their combinations, in conjunction with sensitivity analyses for spatial effects. Habitat complexity (foliage height diversity index) and temperature were locally measured; surface area available within 200 m elevational intervals was obtained using GIS software. We further locally surveyed insect biomass and related it to species richness of insectivorous birds.

**Results:** Birds displayed a monotonic decline in species richness (from 113 to 35 bird species) with increasing elevation, and a nested pattern of species loss. The observed patterns were best explained by habitat complexity for the insectivores, frugivore-insectivores, and total number of bird species. The available surface area was the best predictor for frugivorous birds. The mean temperature had a high correlation with species richness of all birds and gave the best fit of species richness for insectivore-nectarivores and pure nectarivores. The biomass of insectivorous birds correlated with the biomass of arthropods. We ruled out the possibility that the elevational pattern observed in birds could be driven by a single phylogenetic radiation.

**Main conclusions:** We observed species richness patterns correlate well with habitat complexity and mean temperature, but mean temperature was not ranked as high as expected. Our results thus challenge the generally expected high importance of temperature as a regulator of water availability, production, and biochemical process that influence species richness, and underscore the importance of vegetation structure and the food resources as the driver of observed species richness.

## KEYWORDS

altitudinal gradient, climate, diversity, feeding guilds, foliage height diversity, habitat complexity, Papua New Guinea, surface area, temperature

## 1 | INTRODUCTION

Montane regions harbour more than half of the world's biodiversity hotspots and provide an attractive setting for biodiversity studies which has resulted in a notable increase in research on elevational patterns on mountains (e.g., Guo et al., 2013; Lomolino, 2001; Rahbek, 2005). Knowledge on patterns of species richness has steadily improved, yet their interpretation remains contested (Bertuzzo et al., 2016; Wu et al., 2013). Commonly described elevational patterns include: (a) monotonically decreasing richness with elevation, (b) low-elevation richness plateau followed by a decrease with elevation, (c) low-elevation plateau with mid-elevation richness peak, and (d) unimodal mid-elevation peak in species richness (Guo et al., 2013; McCain, 2009; Rahbek, 1995). Species richness rarely increases with elevation along complete gradients (e.g., Martin, 1958; Wang et al., 2011; Wake, Papenfuss, & Lynch, 1992). Surprisingly, little effort has targeted mechanisms driving differences in the elevational patterns of subgroups (e.g., frugivores) comprising of a given taxon (e.g., birds) that could reflect differences in physiological tolerance or niche partitioning among these groups (Gaston, 2000; Guo et al., 2013; Terborgh, 1977). Understanding the mechanisms underlying elevational diversity patterns is critical also for conservation efforts, especially as montane regions are likely to face reorganization of plant and animal communities in response to climate change.

Many non-exclusive hypotheses have been proposed for species richness. Among possible drivers, temperature directly controls biological productivity of the community, which in turn has been linked to diversity (Brown, Gillooly, Allen, Savage, & West, 2004; Clarke & Gaston, 2006; Hawkins, Porter, & Felizola Diniz-Filho, 2003). Higher temperatures also speed up speciation (i.e., "temperature-speciation hypothesis"; reviewed by Brown, 2014), and while a given taxonomic group show complex distribution patterns and respond to different environmental factors, scaling up diversity (i.e., increasing the phylogenetic coverage) to the community level leads to a support for temperature as a main regulator of water availability, production, and biochemical process that influence species richness in both plants and animals (Clarke & Gaston, 2006; Peters et al., 2016).

Other factors observed to correlate with species richness include habitat complexity and foliage stratification (MacArthur & MacArthur, 1961), regional and evolutionary history (e.g., Rahbek & Graves, 2001), regionally available area (Rahbek, 1997), and mid-domain effect (Colwell, Rahbek, & Gotelli, 2005; Colwell et al., 2016—using also the dataset presented here). A local community is also constrained by the species available in a regional species pool (Belmaker & Jetz, 2012; Lessard, Belmaker, Myers, Chase, & Rahbek, 2012; Lessard, Borregaard, et al., 2012; Zobel, Maarel, & Dupré, 1998). Observed patterns might be further influenced by methodological biases, sampling effort (McCain & Grytnes, 2010), or spatial

design of sampling (i.e., completeness of the gradient surveyed and grain; Bhatta, Grytnes, & Vetaas, 2018; Nogués-Bravo, Araújo, Romdal, & Rahbek, 2008).

All else being equal, species richness generally increases with area (McCain & Grytnes, 2010), as large areas promote species coexistence in ecological time and speciation in evolutionary time (Rahbek, 1997; Romdal & Grytnes, 2007). The null hypothesis for elevation trends in species richness is thus a species–area function taking into account generally diminishing area available with increasing elevation.

The present study looks at the site of Mt Wilhelm (the highest mountain of Papua New Guinea with a peak at 4,509 m above sea level [a.s.l.]), where water availability is high across a broad range of elevations. Climate puts restrictions on how many species can survive at different locations (Hawkins et al., 2003; McCain & Grytnes, 2010). Many aspects of climate are potentially important for species richness (e.g., humidity and cloud cover), but the three most commonly studied climate axes are temperature, precipitation, and seasonality (McCain & Grytnes, 2010). We expected that species richness will rapidly decrease as temperature falls (McCain, 2009; McCain & Grytnes, 2010).

The "habitat heterogeneity hypothesis" (MacArthur & MacArthur, 1961; MacArthur, MacArthur, & Preer, 1962; Simpson, 1949) assumes that structurally complex habitats are able to cater for a greater diversity of species. Each species requires a "patch" of vegetation within a particular forest stratum as its microhabitat and the variety of "patches" determines the variety of breeding bird species. A structurally complex habitat will have higher species richness, with habitat structure having more influence than productivity alone. This effect should be strongest for habitat sensitive insectivorous species (Robinson & Holmes, 1982) because habitat complexity may affect insectivorous birds in two different ways: directly via available living or nesting space, and indirectly via the availability of arthropods, feeding on plants, providing resource for birds.

The present study is the first to rigorously document elevational patterns of bird species richness along at Mt Wilhelm, one of the few complete undisturbed elevational gradients of palaeo-tropical rain forest, spanning from the sea level to the timberline. Only a few similar quantitative bird studies have been conducted, for example, in Tanzania (Romdal & Rahbek, 2009), Brazil (Goerck, 1999) and in Peru (Terborgh, 1977). Elsewhere, lowlands are typically heavily disturbed by human activities, or the mountains do not reach timberline. To disentangle the effect of various factors on bird species with different ecologies, we examine species richness of five feeding guilds (insectivores, frugivores, frugivore-insectivores, insectivore-nectarivores, and nectarivores) in the context of their phylogenetical signal. Separately, we investigate the relationship of insectivorous birds to food resources (biomass and abundance of arthropods). The

aim of this study was to find biotic and abiotic drivers of species richness of birds overall and of individual guilds along the rain forest elevational gradient.

## 2 | MATERIALS AND METHODS

Our study was performed on the slopes of Mt Wilhelm (4,509 m a.s.l.) in the Central Range of Papua New Guinea (Figure 1). The complete rain forest gradient extended from the lowland floodplains of the Ramu river (200 m a.s.l., 5°44'S, 145°20'E) to the timberline (3,700 m a.s.l., 5°47'S, 145°03'E; Figure 1). Average annual precipitation is 3,288 mm (local meteorological station) in the lowlands, rising to 4,400 mm at the timberline, with a distinct condensation zone between 2,500 and 2,700 m a.s.l. Mean annual temperature (measured for 1 year by our data loggers) decreases from 27.4°C at the lowland site to 8.37°C at the timberline at a constant rate of 0.54°C per 100 m in elevation. The study was completed along a 30 km long transect (200–3,700 m a.s.l.) with eight sites, evenly spaced at 500 m elevational increments (with maximal spatial extent  $\pm 60$  m elevation). They were selected to represent typical forest habitats of the gradient. Survey tracks at each study site were directed through representative and diverse microhabitats (e.g., ridges, valleys, rivulets, emergent trees, small natural forest gaps, and flat land forest;  $\geq 250$  m from forest edge). The elevational gradient does not have any obvious ecotones. The habitats within surveyed transect could be described as 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.) according to Paijmans (1976). The typical species composition of forest (Paijmans, 1976), general climatic conditions, and individuals study sites are described elsewhere (McAlpine, Keig, & Falls, 1983; Sam & Koane, 2014).

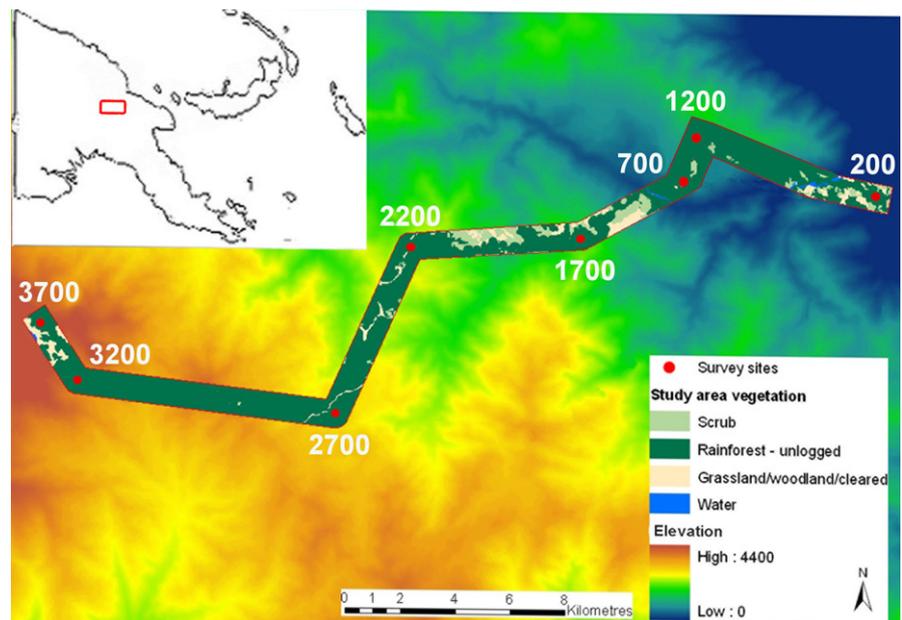
### 2.1 | Bird sampling

Bird communities were surveyed using point counts, mist-netting, and random walks. Bird sampling was conducted under the animal use permits 1315-20424/2012-30, research permit 11800056119 (permitting to hold mist-nets in Papua New Guinea) and banding permit CZ-1062 and AUS-3173. Point counts at each elevational site were carried out at 16 points regularly spaced along a 2,350-m transect (successive points were  $150 \pm 5$  m apart, to avoid overlap, and up to 120 m apart in elevation). All birds seen or heard within a fixed radial distance of 0–50 m (estimated or measured by a laser rangefinder) were recorded. We started surveys 15 min before sunrise, at a randomly selected point and direction to a subsequent survey; such randomizing removed the possible effect of time of day on the number of birds recorded visually or vocally. Each count lasted 15 min so that all 16 points were surveyed before 11:00 (i.e., such survey on all 16 points represents one replication in time). All points and all study sites were surveyed equally.

We also mist-netted birds using a 200 m long line of nets (2.5 m high  $\times$  12–18 m long, 16 mm mesh) from 5:30 am to 5:30 pm daily with checks every 20 min. We set all the mist-netting nets at the same height at all forest sites, so the nets touched the ground and its upper end reached 2.5 m above ground. We identified all mist-netted individuals to species level, marked them with colour bands, and released them within 10 min.

Finally, we walked (2 km/hr) along the existing forest tracks and along the point count transect and recorded a continuous list of species within a 50 m radius from the observer. This method covered c. 80 ha of area. Each walk covered 2–3 km and lasted 2–3 hr per day starting at 3:00 pm. In total, we accumulated 20 hr of random walks per site. All surveys were conducted by three observers (K.S., B.K., and S.J.) in three teams of two observers with rotating membership. All observers have at least 3 years previous experience working with

**FIGURE 1** Study area in Papua New Guinea (red rectangle in the inserted map). White dots denote study sites. The vegetation cover is shown for a 2 km wide buffer zone around the transect line. The vegetation cover was mapped independently from present study and the data for the buffer was provided by Shearman, Ash, Mackey, Bryan, and Lokes (2009) UPNG Remote Sensing Centre, Papua New Guinea



birds in Papua New Guinea. We also recorded vocalizations at each survey point during surveys using a Marantz PMD 620 recorder, (Eindhoven, Holland) and a Sennheiser ME67 microphone (Hanover, Germany). This allowed us to identify any unrecognized bird vocalizations we encountered during our random walks. The combination of team work of skilled observers and recording of vocalization during all surveys allowed us to identify all recorded individuals reliably. We follow the IOC World Bird List (version 6.1., [www.worldbirdnames.org](http://www.worldbirdnames.org)) species-level taxonomy and nomenclature.

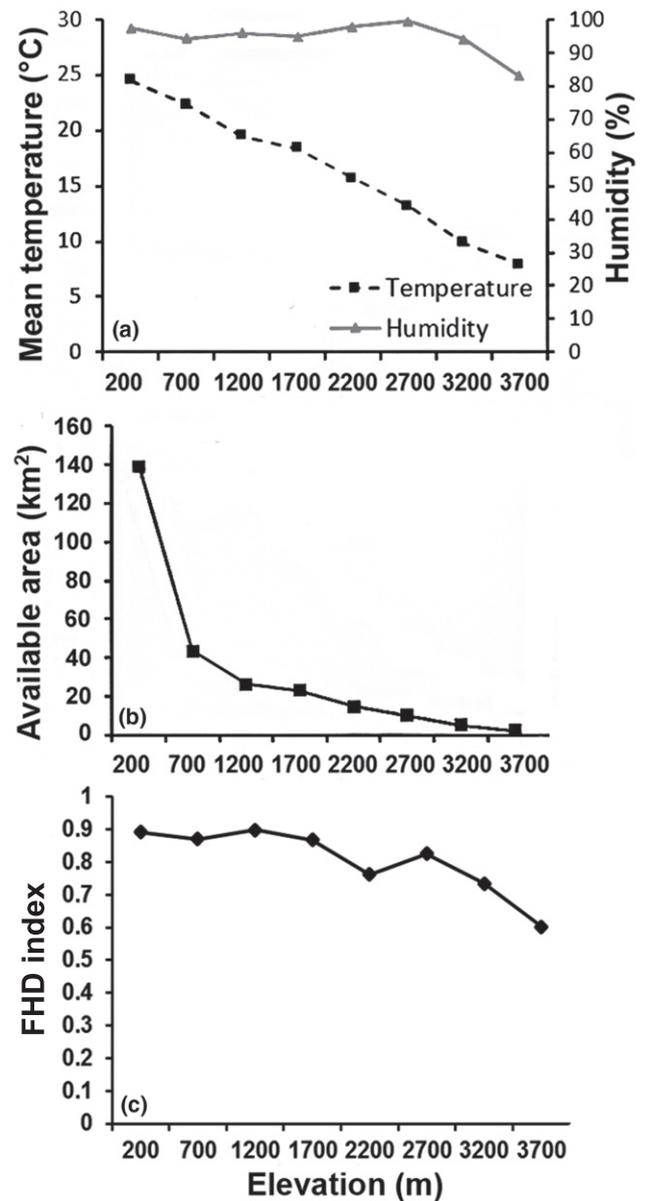
We conducted three surveys during this study: the first survey between 9 April and 31 May 2010 (3 point counts [PC], 3 mist-netting days [MN], 6 random walks [RW]), the second survey between 26 July and 15 October 2010 (6 PC, 5 MN, 10 RW), and the third survey from 15 May to 15 July and from 1 August to 15 October 2012 (5 PC, 3 MN, 4 RW). In total, our dataset for each site included 14 replications (in time) of the 16 point count surveys, 11 mist-netting days, and 20 hr of random walks.

Recorded birds were partitioned into five trophic guilds: insectivores, frugivores, frugivore-insectivores, insectivore-nectarivores, and nectarivores, based on dietary information in standard references (listed in Supporting Information Table S1.1 in Appendix S1). We requested help from three independent specialists on New Guinean avifauna (Andrew Mack, Krystof Chmel and Christophe Thebaud) to classify observed bird species into feeding guilds and consulted our own data (Sam, Koane, Jeppy, Sykorova, & Novotny, 2017) to arrive at the final classification. A system of coarse partitioning does not accurately reflect the feeding preferences according to specialists but provides very similar results (Tvardikova, 2013). Detailed information on feeding preferences, classification, and references are summarized in Supporting Information Table S1.1 in Appendix S1 and by Sam et al. (2017). From the complete list of observed species (Supporting Information Table S1.1 in Appendix S1), all raptors and swifts were excluded (68 individuals of 18 species) as it was difficult to sample them in a standardized manner from the forest interior. Only abundances of understory birds (marked in Supporting Information Table S1.1 in Appendix S1) were used for comparison with food resources in the forest understory.

## 2.2 | Explanatory variables

We used the log-transformed surface area of elevational belts 200 m wide across the whole New Guinea mainland (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) as a proxy for available area (Figure 2). We also investigated the effect of available area using wider elevational belts that were either 400 or 600 m wide. The results differed slightly for individual feeding guilds but wider elevation belts always performed poorly compared to the 200 m belt (Supporting Information Table S1.2 in Appendix S2).

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 at each site (Figure 2). Mean annual temperature decreased at a constant rate of 5.42°C per 1,000 m elevation,



**FIGURE 2** Mean daily temperature and humidity (a), area available for 200 m wide elevational belts (b), and foliage height diversity index (c) at the elevational study sites of Mt. Wilhelm elevational gradient in Papua New Guinea

while mean humidity remained high across the entire gradient (83.0%–99.4%). We therefore used only temperature as a predictor variable.

We derived indices of vegetation structural diversity from measures of five variables using the Shannon–Wiener information index (Clawges, Vierling, Vierling, & Rowell, 2008; Cousin & Phillips, 2008; MacArthur & MacArthur, 1961; MacArthur, Recher, & Cody, 1966). These habitat variables, measured at each point (i.e., 16 per elevational study site, 128 in total), included: (a) Average canopy height (using a laser rangefinder, 3 measures/point). (b) Ground layer density (in 1 × 1 m plots, 15 measures/point, 0–0.5 m in height). (c) Shrub density (using scatter plots, 5 measures/point, 1–3 m height). (d)

Mid-story density (5 photos/point of mid-story, 3–10 m height, photos scored as 0–4; 0 [no vegetation in the stratum], 4 [a dense, closed stratum] August, 1983). (e) Canopy density (5 photos/point analysed in a Gap Light Analyzer; Frazer, Fournier, Trofymow, & Hall, 2001; Figure 2).

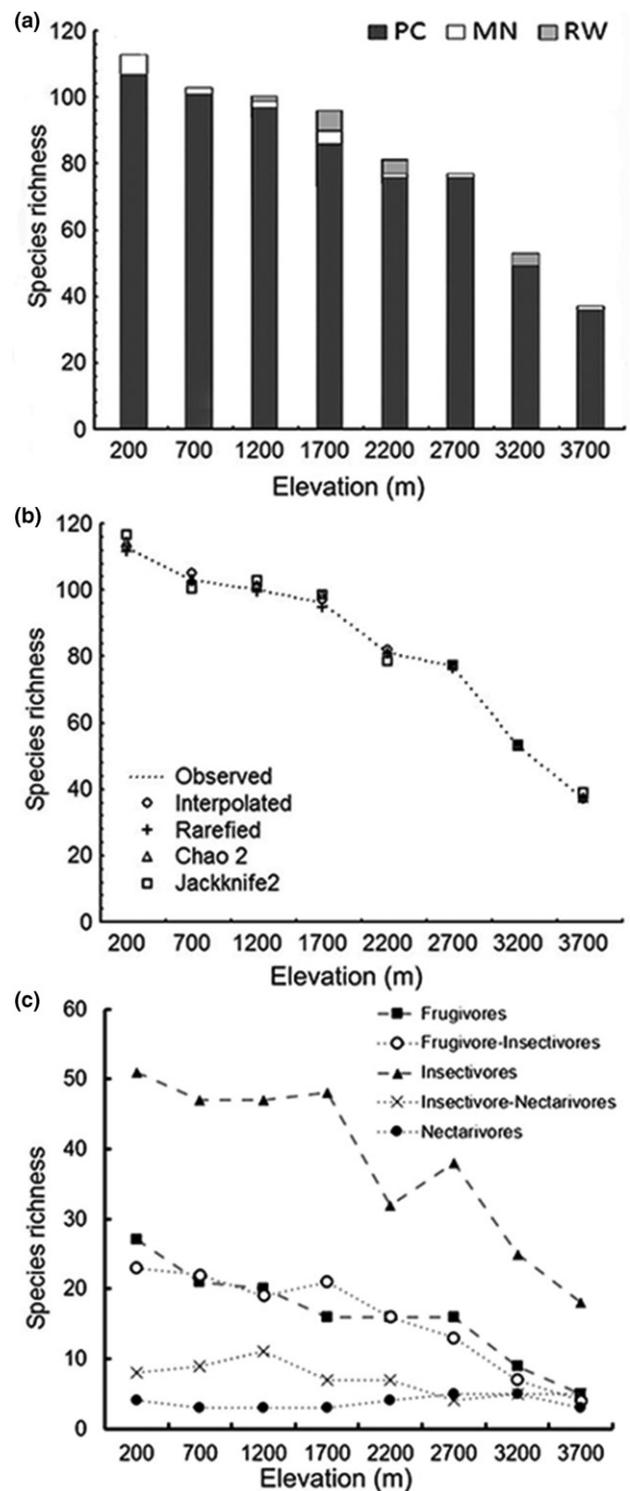
Although the temperature was monitored at only one location per study site, the foliage height diversity (FHD) index (i.e., the habitat complexity covariate) was evaluated at each of the 16 points per site where point count surveys were conducted. Therefore, in view of the observation by Rahbek (2005) that “The definition and choice of scale can directly affect the results of any given analysis...”, we additionally investigated the effect of different spatial scales on the habitat complexity models (Poisson, auto-Poisson, and auto-normal) by applying them to the fine-scale dataset.

To sample arthropods at each elevational study site, we carefully lowered crowns of 20 saplings (3–5 m high) of each of the five selected tree species (K. Sam et al., unpubl. data) growing along the studied transect. Individual saplings were about 100 m apart, their crowns had  $12.2 \pm 2.3 \text{ m}^2$  of foliage (c.  $1,200 \text{ m}^2$  of foliage per each elevation), and the density of saplings similar to those surveyed (i.e., DBH 5–6 cm) was  $30 \pm \text{SD. } 11$  per  $20 \times 20 \text{ m}$  plot at each elevation. We wrapped the whole crowns of saplings into a mosquito net, and fumigated them with fast knockdown insecticide (Mortein®). After the fumigation, we shook the foliage vigorously into the mosquito net, collected all dislodged arthropods into vials filled with ethanol, and visually inspected the foliage for any remaining individuals. Arthropods were identified to order level and their length and width was measured to the nearest millimetre. Order specific equations (Wardhaugh, 2013) were used to calculate the biomass of arthropods per  $10 \text{ m}^2$  of foliage.

We constructed a phylogeny of the species in our dataset based on the freely available data from A Global Phylogeny of Birds (<http://birdtree.org>) accessed on 5 June 2016. We then used the ‘picante’ package (Kembel et al., 2010) and *multiPhylosignal* functions to calculate Blomberg et al.’s (2003) *K*, *phylosig* (Revell, 2012) to calculate Pagel’s (1999)  $\lambda$  (both measuring phylogenetic signal), and *pd* (measuring phylogenetic distance within a group of organisms) to inspect phylogenetic signal and distances within feeding guilds. All data are available on Figshare <https://doi.org/10.6084/m9.figshare.6203312>.

### 2.3 | Statistical analyses

In all analyses, we used the total number of species with standardized area and time from all three surveys. Most of the species were recorded during the point counts. The other methods recorded only a few additional species for each site (Figure 3). The observed species richness is a good index of actual species richness, as long as it is based on sufficient sampling effort. However, other species richness indices (including e.g., standardization by number of individuals recorded) can capture different aspects of diversity and thus produce different results compared to standardized sampling effort (Gotelli & Colwell, 2001). Therefore, we also compared observed species



**FIGURE 3** Bird species richness partitioned according to survey methods (a), observed, rarefied, estimated (Chao2, Jackknife2) and interpolated species richness of all bird species (b) and observed, interpolated, and rarefied species richness of birds partitioned into feeding guilds (c) along elevational gradient of the Mt Wilhelm in Papua New Guinea. PC—point count (a priori selected as the main survey method, all species recorded by PC), MN—mist-netting (species recorded from nets but not PC), RW—random walks (birds observed during random walks but not PC or MN)

richness with other measures of diversity: rarefied, interpolated, and estimated species richness. We used individual-based rarefaction to compare species richness at comparable numbers of individuals (standardized to the number of individuals observed at 3,700 m in ESTIMATES 9.1; Colwell, 2013). For interpolated richness, species were assumed to occur at all intervening elevations between the minimum and maximum elevations recorded (Wu et al., 2013). Such interpolation may create a bias towards falsely higher richness at intermediate elevations in the case of genuine distribution gaps. Furthermore, we used non-parametric estimators (Chao2, Jackknife2) to compute total species richness, using the software ESTIMATES 9.1.

Species richness (total or partitioned into feeding guilds) was used as the dependent variable in Poisson regressions with various combinations of three predictor variables: mean temperature, FHD index, and (log-transformed) area available within 200 m elevational belts. We used  $\Delta AIC_c$ , Akaike weights ( $w_i$ ) and  $R^2$  to interpret regression results and evaluate models and their fits (Anderson & Burnham, 2002). Species richness data and environmental predictors may exhibit significant spatial autocorrelation, which we investigated using Moran's  $I$  with the reciprocal of inter-site distances as weights. The question arises whether spatial effects should be included explicitly in the modelling approach. However, the small number of sites means that (a) spatial models are not ideal for the primary analysis and (b) correlograms of residuals would be unreliable for diagnosing Poisson regression validity. Therefore we conduct a sensitivity analysis for spatial effects by comparing Poisson models to auto-Poisson and auto-normal models (Bardos, Guillera-Arroita, & Wintle, 2015b; Besag, 1974) estimated via maximum pseudolikelihood (Bardos, Guillera-Arroita, & Wintle, 2015a, 2015b). The method is described in detail in Supporting Information Methods S1.1 in Appendix S1. To investigate species turnover and their nestedness, we analysed community data in the 'vegan' package, using the *nest-edtemp* function (which provides the option for plot) and *ecosimu* (*nestedchecker*) in R software (R Core Team, 2013).

### 3 | RESULTS

Our data are based on recordings of 34,587 bird individuals of 234 species (Supporting Information Table S1.1 in Appendix S1) recorded at eight elevational sites on Mt Wilhelm. In total, 232 species and 25,553 individuals were recorded (visually and based on vocalization) during point counts, 1,349 individuals of 103 species were mist-netted, and 7,685 individuals of 193 species were recorded visually and auditorily during random walks (Figure 3). We found that derived measures of species richness (interpolated, rarefied, and estimated) do not differ meaningfully from the observed species richness and therefore we used the observed richness for all analyses. Frugivores were represented by 50 species, frugivore-insectivores by 45 species, insectivores by 111 species, insectivore-nectarivores by 18 species, and nectarivores by 10 species along the whole gradient. The species richness of all birds decreased with elevation from 113 bird species recorded at 200 m a.s.l. to 35 bird species at the

timberline at 3,700 m a.s.l. (Figure 3). The number of species in individual feeding guilds also decreased with elevation (Figure 2).

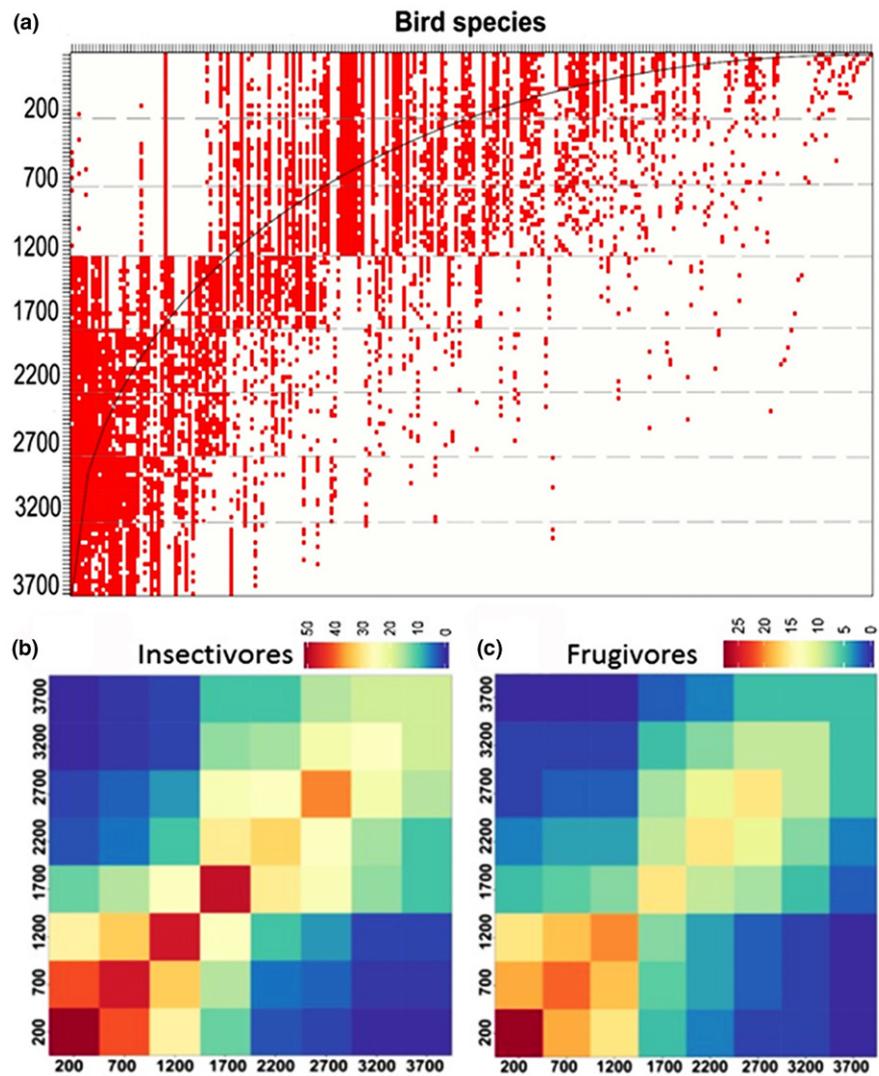
Species loss showed a nested pattern along the gradient, and were significantly nested ( $p = 0.01$ , Figure 4; Supporting Information Figure S1.2 in Appendix S2 for individual guilds). The nestedness for all birds was 25.19 in scale from 0 (totally nested) to 100 (totally random) with matrix fill 0.19, and thus the species were significantly nested. The majority of bird species occurred in lowlands and some of these reached higher elevations. Bird species occurring at high elevations usually had their lower distributional limit at 1,700 m a.s.l. Frugivores and frugivore-insectivorous birds were more nested (nestedness temperature 14.01–16.88) in lowlands than the other three guilds (nestedness temperature  $>26.89$ ; Figure 4, Supporting Information Figure S1.2 in Appendix S2).

Habitat complexity (FHD index) was selected (Table 1) as the best model for overall species richness (lowest  $\Delta AIC_c$ ) and also had the lowest  $\Delta AIC_c$  for insectivores and frugivore-insectivores. Mean temperature models were superior according to the  $\Delta AIC_c$  for insectivore-nectarivores and also (albeit with low  $R^2$ ) for pure nectarivores. Surface area available per elevational belt had the lowest correlation ( $R^2$ ) with total species richness of all models, and was poorer on a  $\Delta AIC_c$  basis than the other basic (single-predictor) models (Table 1). Surface area was selected by  $\Delta AIC_c$  as the best fitting model only for frugivorous birds and its  $R^2$  was generally relatively low (Table 1).

The best fitting models for insectivore-nectarivores and particularly for pure nectarivores were poorer than those for the other guilds or for the total species richness. The insectivore-nectarivores exhibit only a weak trend across the gradient, while for the pure nectarivores, no trend is obvious. Furthermore, unlike all other guilds, the nectarivores' species richness has a negative Moran's  $I$  (Supporting Information Table S2.2 in Appendix S2) and consistent with this (given that the predictors are poor), five of seven auto-Poisson models for this guild have autocovariate parameter  $\hat{\beta}_{\text{auto}} < 0$  (see Supporting Information Methods S2.1 in Appendix S1).

For all guilds except nectarivores, none of the regressions combining multiple explanatory variables explained substantially more variability than simple models (Supporting Information Table S3.2 in Appendix S2). Model performance for nectarivores was poor in general, probably due to low species counts giving poor contrast across the gradient.

From the results for the spatial sensitivity analysis (Supporting Information Table S4.2 in Appendix S2 for basic models and Supporting Information Table S5.2 in Appendix S2 for all combinations of models), it is immediately clear that apart from pure nectarivores, none of the basic models were sensitive to the inclusion of spatial effects: the worst-case change in covariate effect being  $\Delta\% = 19\%$  (insectivore-nectarivores, habitat model) and other cases being generally much smaller. The results (Supporting Information Table S5.2 in Appendix S2) further show that the tendency for non-robustness increases strongly with the number of predictors. Thus both the AIC criterion and robustness to inclusion of spatial autocorrelation tend to favour the single-predictor models against combinations of predictors.



**FIGURE 4** Relationship of mean total biomass (a) and abundance (b) of understory insectivorous birds recorded daily on 12.5 ha of forest in Papua New Guinea with mean total biomass and abundances of arthropods collected from 10 m<sup>2</sup> of foliage in forest understorey at individual elevational study sites. Biomass:  $SS = 9.899$ ,  $F_1 = 24.07$ ,  $p = 0.003$ ; Abundance:  $SS = 7668.$ ,  $F_1 = 9.508$ ,  $p = 0.022$

Moran's  $I$  (Supporting Information Table S2.2 in Appendix S2) for the fine-scale (128-point) habitat complexity index and species richness data indicates much higher spatial autocorrelation than for the coarse-scale (eight-site) datasets, implying strong positive spatial autocorrelation at short ranges, as is typical in ecological data. Nevertheless, auto-model analyses (Supporting Information Table S6.2 in Appendix S2) indicate only mild sensitivity in fine-scale regression results to inclusion of spatial autocorrelation. The high correlation between coarse-scale habitat complexity data and corresponding species richness data is exemplified by the close resemblance between the FHD index curve in Figure 2 and the insectivore curve in Figure 3 (correlation coefficient of 0.969). By contrast, we find that the fine-scale (128-point) habitat complexity data has a much lower correlation (0.488) with insectivore species richness. Poisson regression of the fine-scale data (see Supporting Information Table S6.2 in Appendix S2) yields much smaller  $R^2$  values and covariate regression coefficients (i.e., effect sizes) than for the coarse-scale data (leaving aside the nectarivores). We interpret these results as follows: (a) If a large patch with a given habitat complexity is subdivided into sufficiently small patches, the number of species each can

carry will fall substantially even if their complexity is only slightly lower relative to the large patch. Thus, the species richness versus complexity relationship is also a function of patch size: smaller patches cannot realize the full potential that their complexity allows on larger scales. (b) Species richness recorded at each of the eight study sites is an accumulation of that recorded at the 16 points within the site (as well as from other methods such as netting). Species that are present in small numbers or that are otherwise difficult to detect will be much more likely to be detected at "one or more" of the 16 points than at all of them. Thus the records for each point would be expected to understate the species richness to a much greater extent than the cumulative record for the site and in that sense would contain less signal and more noise. These errors are always in the direction of understating species richness and thus reducing the apparent effect of informative covariates.

The biomass of purely insectivorous birds occupying forest understorey decreased by 50% between the lowest and highest elevational study sites (Figure 5). This trend was closely correlated with the mean biomass of understorey arthropods ( $SS = 9.899$ ,  $F_1 = 24.07$ ,  $p = 0.003$ ; Figure 5). Correlation between mean

**TABLE 1** Akaike's second-order information criterion ( $AIC_c$ ) for regression models of observed bird species richness along the Mt. Wilhelm elevational gradient in Papua New Guinea, estimated for all bird observations and for the observations divided among five feeding guilds. See Supporting Information Table S2.2 in Appendix S2 for results from a larger set of models featuring combinations of these three models

	$-\log(L)$	$R^2$	Akaike weight ( $w_1$ )	$AIC_c$	$\Delta AIC_c$
All birds					
Mean temperature	28.90	0.94	0.08	64.20	4.06
<b>Habitat</b> (foliage height diversity)	<b>26.87</b>	<b>0.97</b>	<b>0.60</b>	<b>60.14</b>	<b>0.00</b>
Area (log transformed)	30.21	0.91	0.02	66.83	6.69
Frugivores					
Mean temperature	19.65	0.95	0.29	45.70	0.29
Habitat (foliage height diversity)	19.69	0.91	0.28	45.78	0.38
<b>Area</b> (log transformed)	<b>19.50</b>	<b>0.94</b>	<b>0.33</b>	<b>45.41</b>	<b>0.00</b>
Insectivores					
Mean temperature	24.41	0.90	0.09	55.22	4.31
<b>Habitat</b> (foliage height diversity)	<b>22.25</b>	<b>0.98</b>	<b>0.75</b>	<b>50.90</b>	<b>0.00</b>
Area (log transformed)	25.02	0.87	0.05	56.44	5.53
Frugivore-insectivores					
Mean temperature	20.15	0.91	0.35	46.69	0.26
<b>Habitat</b> (foliage height diversity)	<b>20.02</b>	<b>0.91</b>	<b>0.39</b>	<b>46.44</b>	<b>0.00</b>
Area (log transformed)	21.02	0.86	0.14	48.44	2.01
Insectivore-nectarivores					
<b>Mean temperature</b>	<b>16.17</b>	<b>0.74</b>	<b>0.38</b>	<b>38.75</b>	<b>0.00</b>
Habitat (foliage height diversity)	16.51	0.69	0.27	39.42	0.68
Area (log transformed)	16.55	0.63	0.26	39.51	0.76
Nectarivores					
<b>Mean temperature</b>	<b>13.36</b>	<b>0.33</b>	<b>0.32</b>	<b>33.13</b>	<b>0.00</b>
Habitat (foliage height diversity)	13.44	0.10	0.30	33.28	0.15
Area (log transformed)	13.42	0.18	0.30	33.24	0.12

Bold value indicates the best model

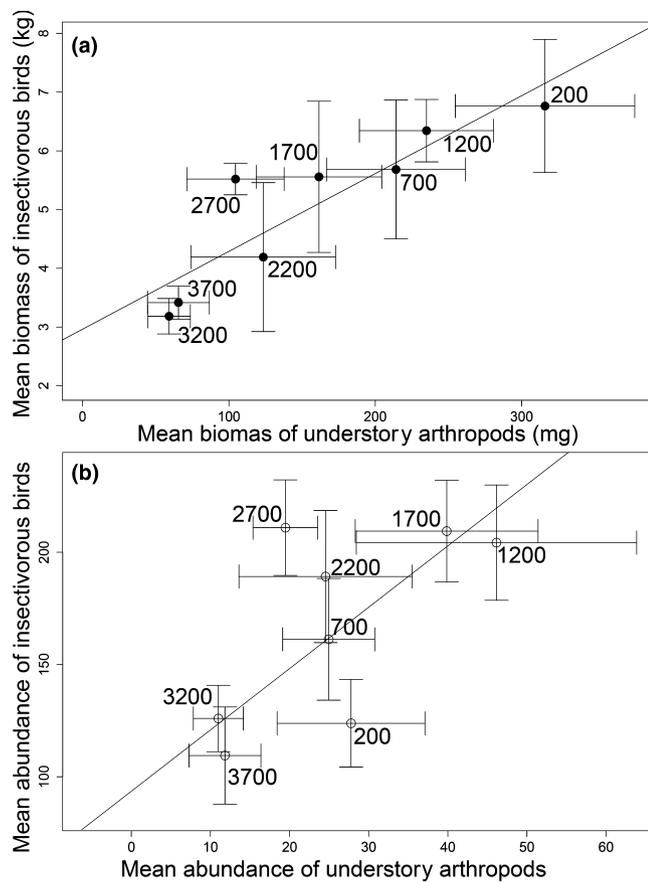
abundances of understory insectivorous birds and abundances of arthropods were more complicated (with the highest abundance at 700 m a.s.l.), weak but still significant ( $SS = 7,668.6$ ,  $F_1 = 9.508$ ,  $p = 0.022$ ; Figure 3). Overall species richness of all insectivorous birds was quite well correlated with biomass ( $AIC = 56.44$ ,  $R^2 = 0.75$ ,  $AIC_c = 5.54$ ) and abundance ( $AIC = 59.69$ ,  $R^2 = 0.61$ ,  $AIC_c = 8.79$ ) of arthropods collected in the forest understory, considering the low number of  $df$  (refer to rest of the models for insectivorous birds compared in Table 1).

The observed birds belonging to individual guilds were characterized by as  $K = 0.448$  ( $p = 0.025$ ) and  $\lambda = 0.854$  ( $p < 0.001$ ). The relationship between phylogenetic diversity (i.e., minimum spanning tree of studied feeding guilds) and the species richness of guilds was not different, with branch length ranging from 22.78 to 32.9 per guild (increasing with elevation, Supporting Information Results S1.2 in Appendix S2). Phylogenetic signal also did not change significantly with respect to elevational communities ( $K = 0.09$ – $0.14$ ) and mean branch length (29.33–34.87, Supporting Information Results S1.2 in Appendix S2).

## 4 | DISCUSSION

We observed that bird species richness declines with elevation and correlates well with habitat complexity and mean temperature, but mean temperature ranked lower than expected. The monotonous decline in diversity was similar to but slower than that found in ants and butterflies (Colwell et al., 2016), and different from mid-elevation maximum found in geometrid moths (Beck et al., 2017) and ferns (Colwell et al., 2016) along the same gradient. This confirms that individual taxa respond to different driving variables or their combinations (Peters et al., 2016).

Climate has been always strongly and positively linked to diversity (Gaston, 2000; Hawkins et al., 2003; Kaspari, O'Donnell, & Kercher, 2000; Wu et al., 2013). However, three different possibilities should be considered separately: (a) a functional link of climate, such as temperature influencing the rate of utilization of chemical energy of organisms, to bird diversity; (b) an indirect effect of climate, through modification of other variables (e.g., vegetation structure) which in turn impact birds; and (c) an impact of climate (direct or



**FIGURE 5** Occurrence of individual bird species (x-axis) at individual points (16 per elevation) of eight study sites of elevational gradient of Mt Wilhelm in Papua New Guinea. Each red point represents a presence of given species at a particular point. Dashed horizontal lines separate elevational study sites (a). Heat maps showing bird species turnover for two feeding guilds along Mt. Wilhelm gradient, at eight study sites between 200 and 3,700 m a.s.l. Each cell represents the number of species shared between the two elevations given at the horizontal and vertical axes. The diagonal represents the number of species observed at each elevation. For instance, in insectivores, we see c. 50 species detected at 200 m, of which c. 40 was observed also at 700 m; continuing higher (or to the right) from 200 m, the graph shows no shared species between 200 and 3,200, 3,700 m. Based on visual interpretations, frugivores are more nested in lower elevations (200–1,200 m) than insectivores and 1,700 m a.s.l. represents an intermediate elevation where lowland and highland species meet

indirect) that is modified by an entirely different factor (such as land area). Clearly, habitat structure is a major covariate of productivity, as three-dimensional vegetation complexity increases with available energy. Willson (1974) and Hurlbert (2004) found that avian richness increased with foliage and vegetation diversity, consistent with the Resource Specialization Hypothesis. This alternative (indirect) explanation for positive species-energy patterns suggests that the number of resource types that can support specialist species increases with productivity (Hurlbert, 2004). Our data seem to support this indirect theory, because the species richness was more closely related to habitat complexity than to mean temperature.

MacArthur and MacArthur (1961) and MacArthur et al. (1962) suggested that vertical stratification and patchiness within a habitat determines the variety of bird species breeding there. This intuitively appealing conclusion that bird species diversity and foliage height diversity are linearly related has not always been substantiated by subsequent work (e.g., Karr & Roth, 1971), but seems to be supported by data from Mt Wilhelm. Similarly, Jankowski et al. (2013) found that tree species composition and vegetation structure were important predictors of bird species composition in the Peruvian Andes. In our results, the habitat model fitted the total empirical species richness much better than mean temperature. The fact that a climatic model underestimates the species richness at elevations where the shrub layer starts to be more pronounced (see Supporting Information Figure S1.1 in Appendix S1) implies that habitat complexity plays an important role for birds. Our data for insectivorous birds further support this conclusion.

Insectivorous birds have been shown to be highly sensitive to habitat structure (Boves et al., 2013; Sekercioglu, 2002) and to changes in availability of microhabitats (Stratford & Stouffer, 2013) either directly or indirectly via arthropods living and feeding on the foliage. We confirmed also the indirect effect of habitat by showing that the biomass and abundance of purely insectivorous birds occupying the forest understorey of Mt Wilhelm was closely correlated with the mean biomass and abundance of understory arthropods. Similarly, food availability was shown to be the most important predictor of species richness for a study along an elevational gradient of Mt Kilimanjaro for both insectivores and frugivores (Ferber, Schleuning, Hemp, Howell, & Böhning-Gaese, 2014) and that vegetation structure had the strongest overall effect on species richness of insectivorous birds only. Their conclusions are thus slightly different from our results, showing that vegetation structure was significant for both frugivore-insectivores and insectivores, while vegetation diversity was a slightly worse predictor than insect biomass (and abundance) for insectivorous birds. Nevertheless, the two studies (this and Ferber et al., 2014) agree that vegetation structure and food availability had the most important effect on pattern in species richness of insectivorous birds and overall species richness. Similarly, Ghosh-Harinar and Price (2014) found that the species richness of foliage gleaners along an elevational gradient was limited by climate via its effects on available food resources. Price et al. (2014) further reported that species richness of insectivorous birds “strikingly” matches the abundances of insects (a pattern very similar to what we see in our data) without providing further statistical tests.

Empirical species richness of frugivorous birds corresponded well with the available surface area of the 200 m wide elevational belt. The species richness of frugivorous birds decreased approximately linearly from 200 to 2,700 m a.s.l., and then decreased more steeply from 2,700 m a.s.l. towards the timberline. Interestingly, species richness of strict frugivorous birds coincided with observed species richness pattern of *Ficus* trees along the gradient (L. Sam, unpubl. data), and with elevational range limits between 2,700 and 3,200 m on the slopes of Mt Wilhelm. Some authors (Goodman & Ganzhorn, 1997; Kissling et al., 2007) have proposed a strong relationship between

the species richness of *Ficus* trees and the entire guild of strict frugivores. Seventy-five per cent of strict frugivores feed on figs, while at least 68 bird species of Mt Wilhelm are known to feed on figs (Shanahan et al., 2001) and the detailed relationship between Frugivores and fruit availability is currently undergoing study in this location.

Lowland forests represent a large share of the surface area of mainland New Guinea (67% of the total area is below 500 m a.s.l.), while the montane surface area decreases very sharply with increasing elevation compared to 0–500 m. The indirect effect of area on elevational pattern of species richness in New Guinea was, to our knowledge, first discussed by Beehler (1981). The hypothesis of an indirect effect of area on species richness was developed theoretically (Storch, Evans, & Gaston, 2005) and for different regions (Romdal & Grytnes, 2007), and confirmed and discussed for example by Wu et al. (2013). In concordance with the indirect area effect hypothesis, we found a strong, but not perfect, correlation between available area (log transformed) and local species richness, indicating the importance of other factors. We hypothesize that a similar principle affected our results as we observed a stronger effect of area on usually highly mobile frugivorous birds than on usually sedentary insectivorous birds.

The results of the present study must be interpreted with caution. Firstly, some biotic, habitat or historical variables (e.g., biotic interactions, evapotranspiration, and occult precipitation) for which no data were available may be important. Secondly, multiple regressions are very sensitive to the pattern of both species richness and explanatory variables; a small change in variables may bring a significant change in regression results, especially when the number of study sites along the elevational gradient is limited, and when degrees of freedom is low as it was in our case.

In conclusion, birds along an elevational gradient of Mt Wilhelm displayed a monotonic decline in species richness, and a nested pattern of species loss with increasing elevation. Frugivorous birds are more nested in lower elevations than insectivores and 1,700 m a.s.l. represents an intermediate elevation where lowland and highland species meet. The eastern slope of Mt Wilhelm represents a wet tropical montane habitat. Thus, unsurprisingly, the pattern of decreasing species richness was consistent with those found in other studies of birds in New Guinea as well as in other wet tropics (e.g., Kikkawa & Williams, 1971: New Guinea; Terborgh, 1977: Peruvian Andes). In contrast to other studies on birds in wet tropics (McCain, 2009), we did not find climate variables or available surface area (Beehler, 1981) to be the main direct driver of species richness. The present study rather indicates that overall species richness is driven by habitat complexity and food availability (for closely studied insectivorous birds). It is interesting to note that the resulting species richness is an accumulation of the species richness of individual feeding guilds, yet habitat was the best explanatory variable for only two of the five guilds. As such, our results thus challenge the generally expected high importance of temperature as a regulator of water availability, production, and biochemical process that again influence species richness, and underscore the importance of vegetation

structure and the availability of food resources as the indirect driver of observed species richness.

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## BIOSKETCH

**Katerina Sam** is an ecologist broadly interested in relationships between predators and arthropods. This work represents a component of her PhD at the University of South Bohemia in the Czech Republic. She and her colleagues and assistants collaborated on investigating the biodiversity of birds and arthropods along elevational the Mt Wilhelm gradient.

Author contributions: K.S. and V.N. conceived the ideas, K.S., B.K., and S.J. conducted the fieldwork, K.S. and D.C.B. analysed the data, K.S. wrote the manuscript with the help of V.N., and D.C.B. wrote the Supplementary Methods++ and contributed to the manuscript.

## SUPPORTING INFORMATION

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

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