Biomass, abundances, and abundance and range size relationship of birds along a rainforest elevational gradient in Papua New Guinea (#39040)

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Biomass, abundances, and abundance and range size relationship of birds along a rainforest elevational gradient in Papua New Guinea

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The usual positive inter-specific relationship between range size and abundance of local populations was shown to have notable exceptions in Afrotropical montane areas, where range-restricted bird species are unusually abundant. We tested how the local abundances of passerines and non-passerine of Mt Wilhelm elevational gradient in Papua New Guinea relate to their geographic range size. We collected the data on bird assemblages at eight elevations (200 – 3,700 m, 500 m elevational increment) using a standardized point count at 16 locations per elevation. We partitioned the birds into feeding guilds, and we obtained data on range sizes from Bird-Life International data zone. We observed positive trends of the abundance and range size relationship in lowland changing to negative trends towards higher elevations. The total assemblage abundances showed a hump-shaped pattern, with passerine birds, namely then passerine insectivores, driving the observed pattern. In contrast to abundances, the mean biomass of the bird assemblages decreased with increasing elevation (i.e., showed opposite pattern than mean abundances). Our data suggest that montane bird species have abilities to maintain dense populations which compensate for a lower area available near mountain tops.

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Abstract

The usual positive inter-specific relationship between range size and abundance of local populations was shown to have notable exceptions in Afrotropical montane areas, where range-restricted bird species are unusually abundant. We tested how the local abundances of passerines and non-passerine of Mt Wilhelm elevational gradient in Papua New Guinea relate to their geographic range size. We collected the data on bird assemblages at eight elevations (200 – 3,700 m, 500 m elevational increment) using a standardized point count at 16 locations per elevation. We partitioned the birds into feeding guilds, and we obtained data on range sizes from Bird-Life International data zone. We observed positive trends of the abundance and range size relationship in lowland changing to negative trends towards higher elevations. The total assemblage abundances showed a hump-shaped pattern, with passerine birds, namely then passerine

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Introduction

An extensive literature has been devoted to the patterns of species diversity along elevational gradients (McCain 2009; Rahbek 1995). In 2009, McCain reviewed 150 datasets along elevational gradients and found that birds display four distinct diversity patterns in nearly equal frequency on mountains: decreasing diversity, low-elevation plateaus, low-elevation plateaus with mid-peaks, and unimodal mid-elevational peaks. Biodiversity richness of elevational gradients thus triggered further attention of many scientists, while many aspects of bird assembly remain unknown. These studies of species richness have been rarely combined with the study of bird abundance and biomass, arguably more important parameters when it comes to the impact of birds on other trophic levels (but see e.g., Romdal 2001; Terborgh 1977). Even fewer studies have combined these attributes of bird communities with an estimate of available resources (Ding et al. 2005; Ghosh-Harihar 2013; Price et al. 2014) and/or available area along the mountain ranges (e.g., Ferenc et al. 2016).

Many studies did not pay attention to potential differences between passerine and non-passerine species, or passerine species were considered only. Klopfer & MacArthur (1960) suggested that phylogenetically younger passerines should be relatively more abundant in unstable environments. They also showed that the proportions on non-passerines increased from the north towards the tropics, where the conditions are more favorable for the existence of non-passerines. In our work, we aimed to test an analogous hypothesis that the non-passerines will be more abundant in favorable tropical lowlands with stable climatic conditions compared to the higher elevations with less favorable environments. In the Himalayas, the ratio of passerines to non-passerines increased very slowly between 160 and 2,600 m a.s.l., and abruptly between ca. 3,000 – 4,000 m a.s.l. (Price et al. 2014) (but note that not all non-passerines were surveyed). Similarly, passerine abundance increased relative to non-passerines with increasing elevation in the Andes (Terborgh 1977).

The patterns of abundance or biomass in different feeding guilds with elevation have been rarely investigated in birds. However, they are essential for our understanding of ecosystem dynamics and function; arguably, birds as such do not share many ecological functions (Sekercioglu 2006). Along many elevational gradients, insectivorous birds are the most abundant of all feeding guilds (Ghosh-Harihar 2013; Price et al. 2014; Terborgh 1977)

The ability of the species to occupy large ranges might also affect their abundances within the range. Macroecological studies have revealed a pervasive positive interspecific correlation between range sizes and abundance in local populations (Gaston 2000; Gaston & Blackburn 2000). Recently, it has been shown that the majority of positive abundance range-size relationships have been demonstrated on datasets from temperate regions (but see (Blackburn et al. 2006)). Ferenc et al. (2016) discussed that the rule is systematically violated in avian assemblages in African montane forest environments (Reif et al. 2006), where range-restricted species are generally more abundant than species with large ranges (Fjeldså et al. 2012). Several other recent studies of tropical montane taxa report that abundance is uncorrelated with (or negatively correlated to) range size (Nana et al. 2014; Reeve et al. 2016; but see Theuerkauf et al. 2017). The only existing study on this topic from Papua New Guinea showed that abundance (capture rates) was not related to range size (measured as elevational breadth; Freeman 2018).

Factors underlying high abundances of montane forest species remain unknown, but several mutually non-exclusive hypotheses have been discussed (Ferenc et al. 2016). These are: (1) Long-term eco-climatic stability facilitates ecological specialization, which then leads to high local abundances of montane species (Fjeldså et al. 2012). (2) Density compensation in species-poor communities at high altitudes results in high abundances of montane species (MacArthur 1972). (3) Locally abundant tropical montane species survive despite their small range sizes. While insufficiently abundant species get extinct (Johnson 1998).

In this study, we focused on bird assemblages along the elevational gradient of Mt. Wilhelm in Papua New Guinea. The specific goals were to investigate (1) trends in abundances of birds along the elevational gradient, (2) changes in relative abundances of different groups of birds (passerines and non-passerines, various feeding guilds), and (3) effects of range sizes on the abundance of individual species.

Materials & Methods

The study was performed along of Mt Wilhelm (4,509 m a.s.l.) in the Central Range of Papua New Guinea (Figure 1a, b). The complete rainforest gradient spanned from the lowland floodplains of the Ramu river (200 m a.s.l., 5° 44’S 145° 20’E) to the timberline (3700 m a.s.l., 5° 47’S 145° 03’E; Fig. 1). We completed the study along a 30 km long transect, where eight sites were evenly spaced at 500 m elevational increments. Because of the steep terrain, elevation could deviate by 50 m within each study site. Survey tracks and study sites at each elevation were directed through representative and diverse microhabitats (e.g., ridges, valleys, rivulets; ≥ 250 m from forest edge). Average annual precipitation is 3,288 mm in the lowlands, rising to 4,400 mm at 3,700 m a.s.l., with a distinct condensation zone around 2,500 – 2,700 m a.s.l. Mean annual temperature typically decreases at a constant rate of 0.54°C per 100 elevational meters; from 27.4°C at the lowland site (200 m a.s.l.) to 8.37°C at the tree line (3700 m a.s.l.). The habitats of the elevational gradient could be described as lowland alluvial forest (200 m a.s.l.), foothill forest (700 and 1,200 m a.s.l.), lower montane forest (1,700 – 2,700 m a.s.l.), and upper montane forest (3,200 and 3,700 m a.s.l.; according to Paijmans (1976). The plant species composition of forest (Paijmans 1976), general climatic conditions (McAlpine et al. 1983) and habitats at individual study sites (Sam & Koane 2014) are described elsewhere.

Data on bird communities were collected in 2010, 2011 and 2012 during the wet and dry seasons, using a standardized point-count at 16 locations per elevation (Sam & Koane 2014; Sam et al. 2019) where other survey methods and complete species list are presented). The surveys were conducted in the mornings between 5:45 and 11:00 am. Each of the 16 sample points had a radius of 50 m (area 0.785 ha per point, which makes 12.56 ha per elevational study site). Points were located 150 m apart to diminish the risk of multiple encounter of individuals. Each point was visited on 14 different days. The order of the points was changed during each re-survey, to avoid biases due to daytime. Birds were detected for 15 minutes during each visit at each point. This resulted into 240 minutes of daily surveys. During the point-counts, a distance sampling protocol was used, with birds recorded in five 10-m-wide radial distance bands (Buckland et al. 2001). Application of detection adjustments are however generally problematic in tropics (Banks-Leite et al. 2014), and we therefore, used the observed abundance estimates instead of the distance sampling-based estimates in the analyses (see similar reasons and discussion by Ferenc et al. 2016).

We recorded the mean number of individuals of a species recorded at 15-min interval (for all 16 points together) as "mean elevational abundance". Elevations between minimal and maximal range where birds were missing were not considered, i.e., data were not extrapolated. The summed abundances of birds in assemblages at a given elevational site (hereafter "total abundance") were calculated as the sum of mean elevational abundances of all species present. The taxonomy used followed the International Ornithological Congress World Bird List version 6.1.

The elevational mean-point (i.e., optimal elevational distribution of the species) was calculated from the lower and upper elevational limit of a species distribution on Mt. Wilhelm. We divided the species into three exclusive groups according to the position of their elevational mean-point as follows: (a) species having their elevational mean-point in the lower third of the elevational gradient (up to 800 m a.s.l.) were included in the "lowland" group, (b) species with mean-point between 800 and 1600 m a.s.l. comprised the "middle" group, and (c) species with their mean-point in the upper third of the gradient (above 1,600 m a.s.l.) represented the "montane" species group. Note that species (N [illegible]) occurring from along the complete gradient (200-3,200 m) thus fall into the group of montane species. The mean-point and mid-point of elevational range differed slightly (max 640 m) for 22 species. Mean-point moved 13 species from middle to montane group and 9 from lowland to middle group.

All recorded bird species were partitioned into five trophic guilds: insectivores, frugivores, frugivores-insectivores, insectivores-nectarivores and nectarivores based on dietary information in standard references (Hoyo et al. 1992-2011; Pratt & Beehler 2015) and our data (Sam et al. 2019; Sam et al. 2017). Abundances of passerines and non-passerines and individual feeding guilds were compared by non-parametric Kruskal-Wallis tests. We report mean ± SE and abundances per 12.56 ha recorded in 15-minute-long census unless we state otherwise. Range sizes of all birds were obtained from Bird-Life International data zone web pages accessed in July 2016. Bodyweight (mean for males) of the birds were obtained from Hoyo et al. (1992-2011). Bird metabolism was calculated from bodyweight according to available equations (McNab 2009).

Results

In total, we recorded 25,715 birds belonging to 249 bird (Supplementary Table S1) species during the point-counts along the elevational gradient of Mt. Wilhelm during this project. Total bird species richness seemed to show a plateau at lower elevations (up to 1700 m a.s.l.) and decreased with increasing elevation afterward (Figure 2a) (see also Marki et al. 2016; Sam & Koane 2014; Sam et al. 2019) for further results). In contrast, total abundance of birds showed a humped shaped pattern, peaking between 1,700 and 2,700 m a.s.l. with ca. 420-450 individuals of all birds per 16 sampling points (i.e., 12.86 ha) (Figure 2c).

Passerines and non-passerines

Passerines were overall more species rich along the elevational gradient, represented by 161 species in comparison to non-passerines represented by 88 species (Figure 2b). We observed a linearly decreasing pattern in species richness of non-passerine birds ($y = -5.9167x + 60.056$, $R^2 = 0.96$) along the elevational gradient and a hump-shaped pattern ($y = -2.1012x^2 + 18.982x + 27.315$, $R^2 = 0.92$) in species richness of passerine birds (Figure 2b). The species richness of both passerines and non-passerines correlated significantly with their total abundances (r = 0.82 and 0.84, P = 0.013 and 0.008 respectively) (Figure 2 b, c).

Mean elevational abundances of passerine birds were overall significantly higher (4.16 ± 0.25) than mean elevational abundances of non-passerines (3.12 ± 0.3; U = 5128; $Z_{88,161} = -3.59$, $P < 0.001$). The number of individuals per bird species increased continually with elevation, with approximately 2.5 times as many individuals per non-passerine species and nearly twice as many individuals per passerine species at the highest elevation as in the lowlands (Supplementary Figure S1). The mean elevational abundances of passerine birds (calculated as the average of elevational abundances across occupied elevations) of individual species increased with their elevational mean-point (Kruskal-Wallis test: $\chi^2 = 6.16$, df = 2, 161, P = 0.046, Figure 2d). Passerine birds having their elevational mean-point in the montane forest (above 1600 m a.sl.) had the highest mean elevational abundances (Figure 2d), but the smallest range-sizes (Figure 3a). We found no significant change (Kruskal-Wallis test: $\chi^2 = 0.95$, df = 2, 88, P = 0.62) in mean elevational abundances of non-passerine birds with elevational mean-point (Figure 2d) but similarly to passerines, non-passerines with higher elevational midpoint had smaller ranges (Figure 3b). The relationship between local mean abundance and range size across all bird species of the entire forested gradient of Mt. Wilhelm showed a significantly negative trend ($F_{1,248} = 8.22$, P = 0.004). The trends remained negative, albeit nonsignificant, for passerines ($F_{1,159} = 1.17$, P = 0.28) and non-passerines ($F_{1,86} = 2.6$, P = 0.10) separately (Supplementary Figure S2).

Feeding guilds

With respect to which feeding guild they belong, species occurring at low elevations had usually lower mean elevational abundances than species occurring at high elevations (Figure 4a; i.e., their mean elevational abundance increased with increasing elevation). The highest mean abundances had nectarivorous and insectivore-nectarivorous species (Figure 4a) and the pattern was likely driven by presence of flocks of nectar-feeding lorikeets.

Total abundances of birds belonging to different feeding guilds however showed different patterns (Figure 4b). While total abundances of frugivores and frugivore-nectarivores decreased with increasing elevation, total abundance of insectivore-nectarivores and nectarivores showed no trend, and insectivores showed a mid-elevational peak (Figure 4b).

Within passerine birds, the mean elevational abundances of birds belonging to different feeding guilds increased with their elevational mean-point (Figure 4c). In contrast, the mean elevational abundances of non-passerines birds belonging to various feeding guilds showed various patterns (Figure 4d).

Mean biomass of bird communities (Figure 5) recorded at each elevational study site decreased with increasing elevation, showing thus opposite pattern than mean elevational abundances. At the upper most two elevations (3,200 and 3,700 m) mean biomass of passerines was relatively larger than biomass of non-passerines which corresponds partly also with their mean elevational abundances at these elevations (Figure 5a). The decreasing pattern in decreasing biomass was observed both with passerines and non-passerines (Figure 5a), as well as in all feeding guilds (Figure 5b).

Discussion

In this study, we studied the relationships between species richness, abundances, and range sizes in passerine and non-passerine assemblages along a tropical elevational gradient. Avian species richness declines monotonically with elevation on Mt. Wilhelm (Sam et al. 2019). Monotonous decline in species richness is reported to be a typical pattern for wet-based mountains (McCain 2009). However, total abundances of bird assemblages at the individual elevations show a different, a hump-shaped pattern. This is an interesting observation, as previous studies showed that unimodal or linearly decreasing patterns on density paralleled the patterns of total species richness along the same gradients (e.g., Romdal 2001; Terborgh 1977). Our findings are also different from patterns in abundances of birds observed along elevational gradient in Cameroon (Ferenc et al. 2016), where a decline in species richness and uniform abundance of birds were observed with increasing elevation.

The overall pattern in abundance of bird assemblages we observed can be partitioned into a hump-shaped pattern for passerine birds and a decreasing trend for non-passerine birds. Such partitioned patterns correspond better with respective species richness than overall species richness and overall abundance. However, note it might be challenging to interpret patterns non-passerine birds, which represent paraphyletic group of birds. To our knowledge, there is not a single study focusing separately on abundance pattern in passerine and non-passerine birds along an elevational gradient. Our data further show that species richness and abundance of passerines increase relative to non-passerines with increasing elevation. This might be in concordance with previous suggestions that phylogenetically younger passerines should be relatively more abundant in less favorable and stable environments. Klopfer & MacArthur (1960) showed that the proportions of non-passerines towards passerines change from north to south. A study focusing on a similar pattern along an elevational gradient in Himalaya indicated that ratio between abundances of passerines/non-passerines increases only very slowly between 160 and 2,600 m a.s.l., and then increased abruptly between ca. 3,000 – 4,000 m a.s.l. (Price et al. 2014). Unfortunately, this study did not survey all non-passerines (Price et al. 2014).

The widespread pattern that abundance is positively correlated with geographic range size does not seem to apply to New Guinean birds distributed along elevational gradients (Gaston & Blackburn 2000). Contrary to this widely accepted pattern, we found a negative relationship between the local abundance and complete range size of the species. Deviation from positive abundance-area relationship is caused by a combination of a decreasing range sizes and increasing abundances of birds towards high elevations. Such an observation fits to predictions of the density compensation hypothesis, which suggest that in species-poor assemblages, individual species may increase their abundances to fill the available ecological space (MacArthur et al. 1972). Such a hypothesis assumes that extinction filtering removes small-range species that have insufficiently scarce local populations.

We showed that New Guinean bird species with small ranges select for high local abundances, as has been suggested for marsupials in Australia (Johnson 1998), birds of the Australian wet tropics (Williams et al. 2009) or Afromontane birds (Ferenc et al. 2016). There are only few previous examples of datasets that report either nonsignificant or negative abundance–range-size relationships from the temperate zone birds (Gaston 1996; Päivinen et al. 2005), but several studies have reported nonsignificant or negative abundance–range-size relationships from the tropics, both in birds (Ferenc et al. 2016; Nana et al. 2014; Reeve et al. 2016; Reif et al. 2006). However, studies reporting a positive trend (Theuerkauf et al. 2017) or no trend (Freeman 2018) in the tropics also exist.

Avian species richness declines monotonically with elevation on Mt Wilhelm (Sam et al. 2019), which is a typical pattern for wet-based mountains (McCain 2009). However, we show here that the number of individuals per bird species increases with increasing elevation. This observation thus fits to predictions of the density compensation hypothesis, which suggests that in species-poor assemblages, individual species may increase their abundances to fill the available free ecological space (MacArthur 1972; MacArthur et al. 1972). Further investigations of our data and its partitioning into feeding guilds showed that patterns of abundances for passerine birds are driven by insectivorous birds, while frugivores drive the decreasing pattern in non-passerines. This seems to be given solely by species richness of the feeding guild within the two groups of birds. While high proportion of the non-passerine birds of Mt. Wilhelm is identified as frugivores (44%), followed by insectivores (29%), most of the passerines (59%) are insectivorous.

The contrasting pattern for total abundance of passerine and non-passerine bird assemblages and is an interesting fact considering that overall environmental productivity (McCain 2009) and food availability as estimated by abundance of insects or fruits seem to decrease with increasing elevation (e.g., Janzen et al. 1976; Loiselle & Blake 1991), especially along wet mountains like Mt. Wilhelm (McCain 2009). On the other hand, observed patterns in abundances of both groups of birds are parallel to the species richness of these groups along our gradient which corresponds with previously reported results on relationship on abundance and species richness along elevational gradients (Terborgh 1977).

Mean biomass of bird communities recorded at each elevational study site decreased quite steeply with increasing elevation, showing thus opposite pattern than mean elevational abundances. At the upper most two elevations (3,200 and 3,700 m) mean biomass of passerines was relatively larger than biomass of non-passerines which corresponds partly also with their mean elevational abundances at these elevations. The decreasing pattern in decreasing biomass was observed both with passerines and non-passerines, as well as in all feeding guilds. The decrease in biomass suggest decrease in energy flux into the birds at given elevation, very likely because of reduction of primary productivity (Dolton & de L. Brooke 1999).

Conclusions

In conclusion, our data show that passerines and non-passerines have different patterns of species richness and total abundance along the same elevational gradient. In direct contrast to abundance-area relationship hypothesis investigated here, the mean elevational abundances of passerine and non-passerine birds follow a similar trend (significant for passerines, but nonsignificant for non-passerines), with montane birds having a higher abundances then lowland birds. Abundances of passerines driven seem to be driven by insectivores, while non-passerines seem to be driven by frugivores.

Acknowledgments

We wish to thank numerous field assistants from Kausi, Numba, Bundi, Bruno Sawmill, Sinopass, and Kegesugl for help in the field and hospitality.

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Figure 1

Location of the elevational gradient of Mt. Wilhelm in Papua New Guinea (a) and the study sites along the gradient (b).

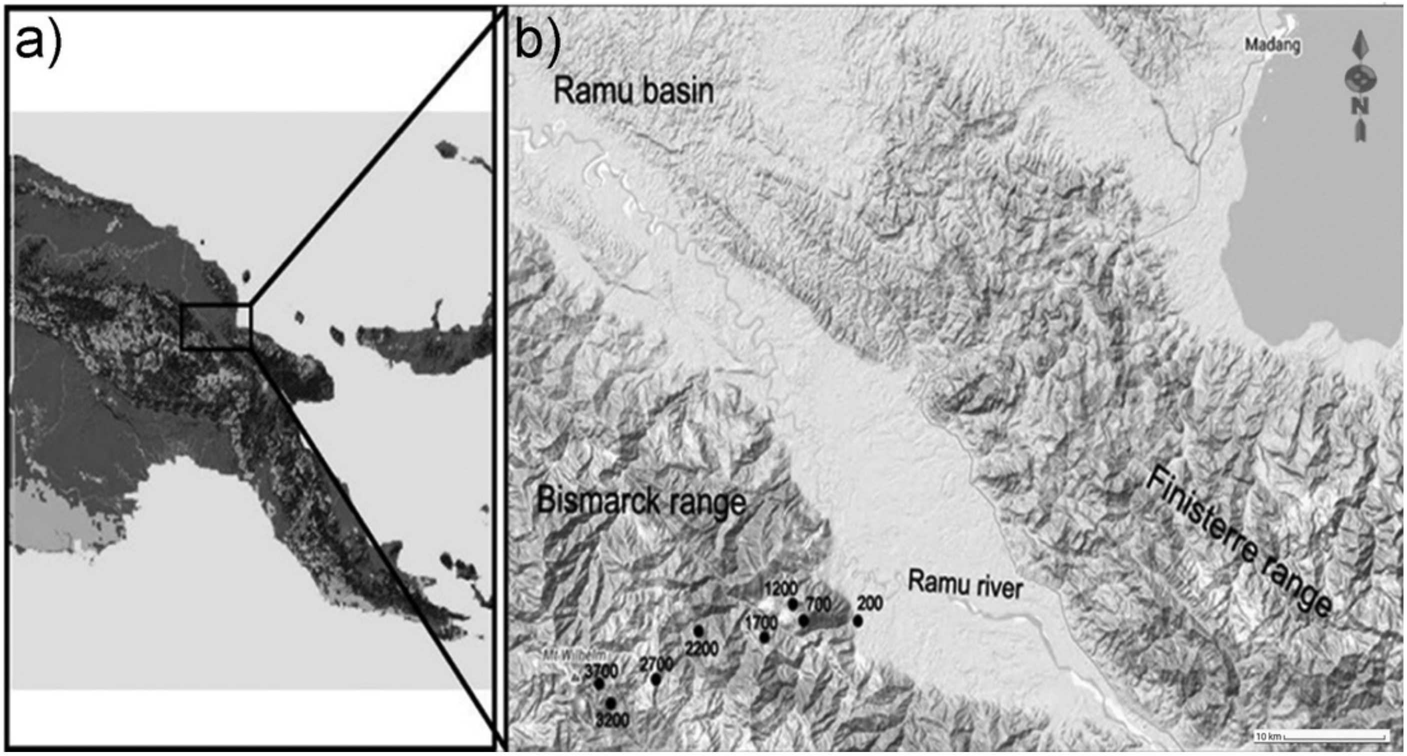

Figure 2

Bird species richness and abundance of birds recorded during point-counts from along the elevational gradient of Mt. Wilhelm.

Bird species richness (**a**, fitted with exponential function: $y = -2.4107x^2 + 11.756x + 93.946$, $R^2 = 0.95$) of all birds recorded during point-counts from along the elevational gradient of Mt. Wilhelm; species richness of passerine and non-passerine birds separately (**b**). Total abundance of passerine and non-passerine birds (left axis, lines) and all birds together (right axis, grey bars) (**c**) and mean elevational (±S.E.) abundance of all passerine and non-passerine species (**c**). Mean elevational abundance of passerine and non-passerine species divided into the three groups based on the position of their mid-point of elevational distribution on Mt. Wilhelm (**d**; Kruskal-Wallis test: passerines $\chi^2 = 6.16$, *df* = 2, 161, $P = 0.046$ and non-passerines $\chi^2 = 0.95$, *df* = 2, 88, $P = 0.62$). Part d) reports mean, conf. int., non-outlier range. Lowland group = elevational mid-point up to 800m a.s.l., middle group = elevational mid-point between 801 and 1600m a.s.l., and montane group = elevational mid-point above 1600 m a.s.l.

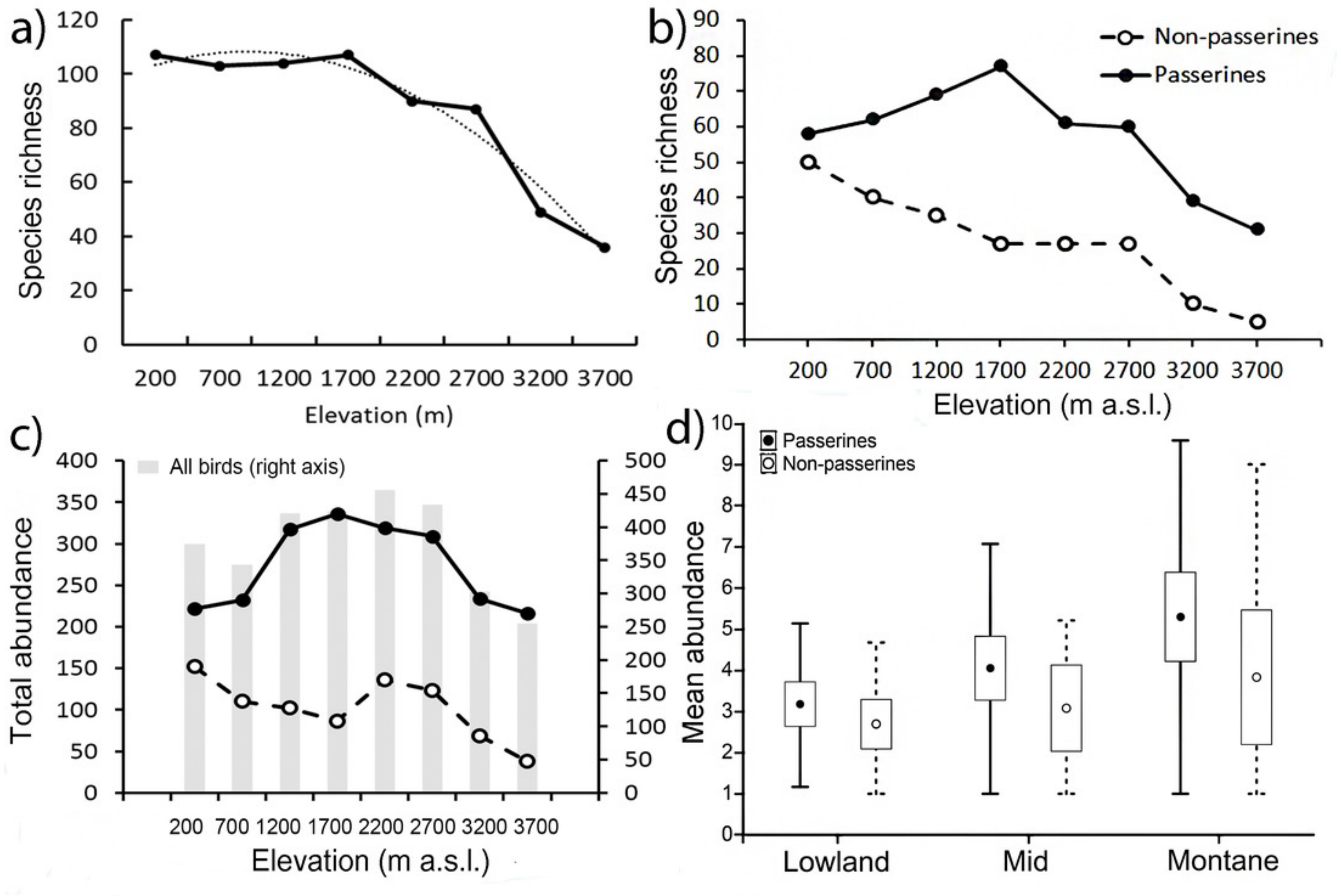
a)
Species richness
120
100
80
60
40
20
0
200 700 1200 1700 2200 2700 3200 3700
Elevation (m)
b)
Species richness
90
80
70
60
50
40
30
20
10
0
Non-passerines
Passerines
200 700 1200 1700 2200 2700 3200 3700
Elevation (m a.s.l.)
c)
Total abundance
400
350
300
250
200
150
100
50
0
All birds (right axis)
500
450
400
350
300
250
200
150
100
50
0
200 700 1200 1700 2200 2700 3200 3700
Elevation (m a.s.l.)
d)
Mean abundance
10
9
8
7
6
5
4
3
2
1
0
Passerines
Non-passerines
Lowland
Mid
Montane

Figure 3

Passerine and non-passerine birds divided into three groups based on the position of their midpoint of elevational distribution on Mt. Wilhelm and their range sizes in km^2.

Passerine and non-passerine birds divided into three groups based on the position of their midpoint of elevational distribution on Mt. Wilhelm and their range sizes in km^2. Note log scale used on y-axis. Passerines: Kruskal-Wallis $\chi^2 = 88.45$, df = 2, N = 161, $P < 0.001$, non-passerines: Kruskal-Wallis $\chi^2 = 23.14$, df = 2, N = 88, $P < 0.001$. Lowland group = elevational mid-point up to 800m a.s.l., mid group = elevational mid-point between 801 and 1600m a.s.l., and montane group = elevational mid-point above 1600 m a.s.l.

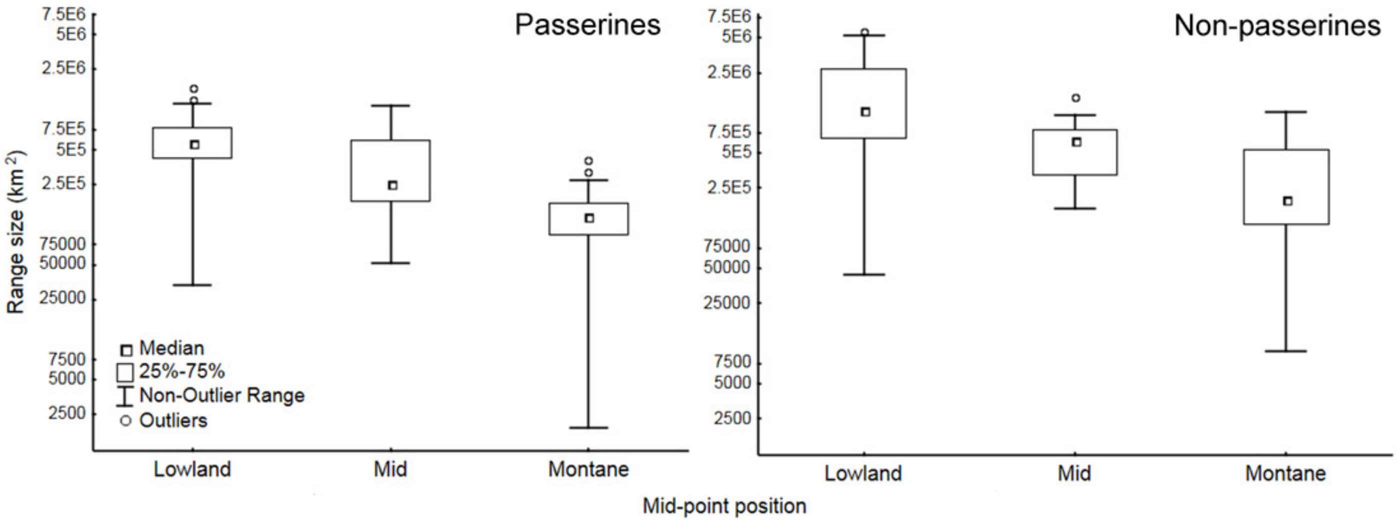

Figure 4

Mean elevational abundances of birds partitioned into feeding guilds (a) and total abundance of bird assemblages partitioned into feeding guilds (b).

Mean elevational abundances of birds partitioned into feeding guilds (a) and total abundance of bird assemblages partitioned into feeding guilds (b). Mean elevational abundances of birds partitioned into feeding guilds and into passerines (c) and non-passerines (d). Ne – Nectarivores, In – Insectivores, In-Ne – Insectivore-nectarivores, Fr – Frugivores, Fr-In – Frugivore-insectivores. Standard errors of the mean are not shown for the clarity of the graph. Lowland group = elevational mid-point up to 800m a.s.l., mid group = elevational mid-point between 801 and 1600m a.s.l., and montane group = elevational mid-point above 1600 m a.s.l.

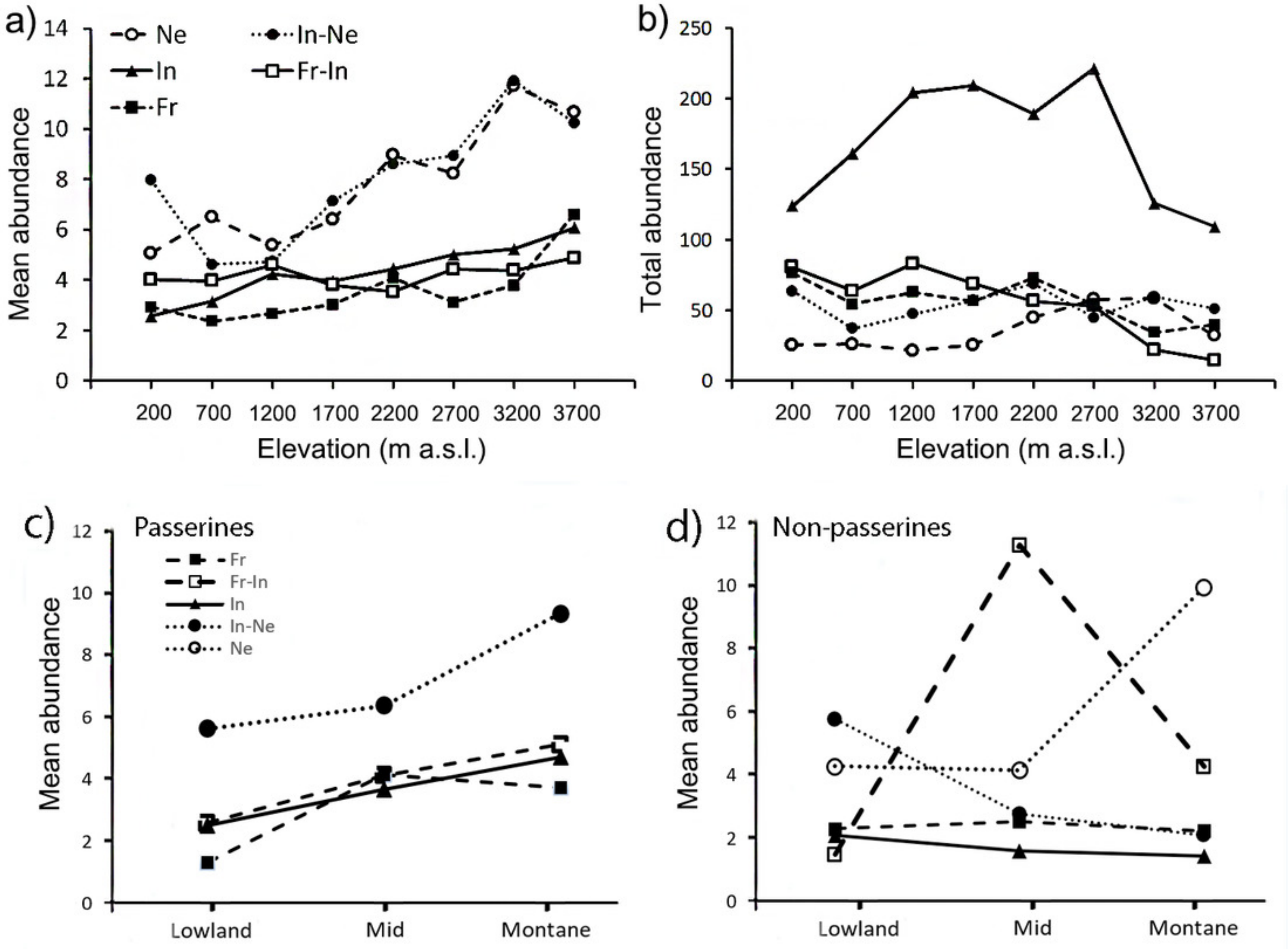
a)
Ne
In
Fr
In-Ne
Fr-In
Mean abundance
0
2
4
6
8
10
12
14
200
700
1200
1700
2200
2700
3200
3700
Elevation (m a.s.l.)
b)
Total abundance
0
50
100
150
200
250
200
700
1200
1700
2200
2700
3200
3700
Elevation (m a.s.l.)
c)
Passerines
Fr
Fr-In
In
In-Ne
Ne
Mean abundance
0
2
4
6
8
10
12
Lowland
Mid
Montane
d)
Non-passerines
Mean abundance
0
2
4
6
8
10
12
Lowland
Mid
Montane

Figure 5

Mean biomass (across the re-surveys of all point-counts) of passerine and non-passerine birds (a) and birds partitioned into feeding guilds (b) of Mt. Wilhelm (biomass in kg/12.86 ha).

Mean biomass (across the re-surveys of all point-counts) of passerine and non-passerine birds (a) and birds partitioned into feeding guilds (b) of Mt. Wilhelm (biomass in kg/12.86 ha).