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Trophic relationships between insectivorous birds and insect in Papua New Guinea

Ph.D. Thesis

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Annotation

The thesis describes diversity of birds along a complete altitudinal gradient and in forest fragments in lowlands of Papua New Guinea. It focuses separately on the diversity of different feeding guilds, and discusses their links to habitat and food resources. More specifically, it focuses on forest insectivorous birds, their predation pressure on arthropods, feeding specializations and preferences, and some of the ways how insectivores search for food.

Declaration [in Czech]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury. Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů, provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalováníplagiátů.

České Budějovice, 30.7.2013

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Kateřina Tvardíková

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List of papers and authors' contributions

The thesis is based on the following papers (listed chronologically):

1. Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea. Tvardikova, K., Novotny, V. (2012) *Journal of Tropical Ecology* 00:1–11 (IF = 1.401)

[KT conceived the study, led fieldwork, analyzed the data and wrote the manuscript with contributions by VN]

2. Herbivore damage increases avian and ant predation of caterpillars along an altitudinal forest gradient in Papua New Guinea. Tvardikova, K., Novotny, V. (Submitted manuscript)

[KT conceived the study, led fieldwork with a help from Bonny Koane, KT analyzed the data and wrote the manuscript with contributions by VN]

3. Diet of land birds along an altitudinal gradient in Papua New Guinea. Tvardikova, K., Koane, B., Jeppy, S., Sykorova, J., Novotny, V. (Submitted manuscript)

[KT conceived the study, KT, BK, SJ led fieldwork, KT, JS analyzed the food samples with contribution of member of research team of VN, KT wrote the manuscript with contributions by VN]

4. Species richness of birds along a complete rainforest altitudinal gradient in the tropics. Tvardikova, K., Koane, B., Novotny, V. (Manuscript)

[KT, VN conceived the study, KT led the field work with contribution of BK, and help from SJ, KT analyzed data with contribution by Carsten Rahbek and David Storch, VN made comments on draft]

5. Disappearance of birds from forest fragments in Papua New Guinea. Tvardikova, K., Koane, B., Novotny, V. (Submitted manuscript)

[KT and VN conceived the study, KT led field work and analyzed the data, BK contributed to field work, KT analyzed the data and wrote manuscript with contribution of VN]

6. New avian records and range shifts of birds along altitudinal gradient of Mt. Wilhelm, Papua New Guinea. Tvardikova, K. (Submitted manuscript)

[KT summarized the data and wrote the manuscript, data resulted from field work along altitudinal gradient and observations were made by KT, BK, SJ]

Authors:

Kateřina Tvardíková [KT] declares that she is the first and corresponding author of all papers, and with major contributions as stated above. The other authors are:

Bonny Koane [BK] – assistant based at New Guinea Research Center, Papua New Guinea, trained by KT in bird identification and insect sorting

Samuel Jeppy [SJ] – village assistant based in Wanang Conservation Area, skilled in bird identification

Jana Sýkorová [JS] – student of Faculty of Science, University of South Bohemia, trained by KT in food sample sorting, canopy openness photograph analyzes, contributed also by literature data gathering

Vojtěch Novotný [VN] – supervisor

Co-author agreement:

Vojtěch Novotný, the supervisor of Ph.D. thesis and co-author of all presented papers, fully acknowledges the contribution of Kateřina Tvardíková as the first author and her major contributions as stated above.

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Author's other paper not included in the thesis, but related to the topic and cited throughout:

Bird abundances in primary and secondary growth in Papua New Guinea: A preliminary assessment. Tvardikova, K. (2010) Tropical Conservation Science 3(4): 373-388 (IF = 0.54)

CONTENT:

Trophic relationships between insectivorous birds and insect in Papua New Guinea

INTRODUCTION

Papua New Guinea and its avifauna

New Guinea is the world's second largest island, after Greenland, covering a land area of 922,000 km^2. Located in the southwest Pacific Ocean, it lies geographically to the east of the Malay Archipelago, with which it is sometimes included as part of a greater Indo-Australian Archipelago. Geologically it is a part of the same tectonic plate as Australia. When world sea levels were low, the two shared shorelines (which now lie 100 to 140 metres below sea level), combining with lands now inundated into the tectonic continent of Sahul, also known as Greater Australia. New Guinea provides a range of habitats from tropical rain forest to glaciers within distances of less than 16 kilometres, a range of altitudes of over 5000 meters, and an equatorial position. The island is divided into southern and northern watersheds, separated by Central Range. In addition, New Guinea has 19 outlying mountain ranges (5 of them off-shore) that vary in size and distance from the Central Range (Diamond 1973). Mainland of New Guinea is represented by the large lowland rainforest areas (44% of the land lies below 100 m asl), as well as high mountain areas (27% of the land lies between 1000 to 4500 m asl).

The rugged topography, which isolates populations in adjacent valleys or on adjacent mountains, has promoted speciation within small areas of a single land mass by essentially the same mechanisms that underlie speciation on large continents (Hall 2002). The number of nonpelagic bird species on the mainland of New Guinea, 513, is large enough to give rise to the complex interactions characteristic of continental faunas, but not so large as to be overwhelming. One of the paradoxes of New Guinea’s biota is the geographical affinities of the flora against the vertebrate fauna. Whereas plant genera have closest affinities to Southeast Asia, ornitofauna is closer to Australian (Beehler *et al.* 1986, Holt *et al.* 2013).

Papua New Guinea (PNG) is political Eastern half of the New Guinea island. Besides the mainland (470,500 km^2), PNG also encompasses over 600 small islands and archipelagos. Mainland of PNG itself houses more than 465 bird species.

Chapters **I, II, V** *and also Tvardikova (2010) represent studies of bird communities at various sites in Papua New Guinea. Chapter* **I** *deals with bird species richness along* *altitudinal gradient in Central Range, chapter* **II** *focuses on altitudinal range distribution of observed species along this gradient and describes some range extensions and species new for the region. Chapter* **V** *and Tvardikova (2010) deal with bird communities in various habitats in lowland forest.*

Altitudinal gradient

Mountains have long captivated mankind and have been considered sacred places in many societies (Bernbaum and Gunnarson 1990), as well as popular destinations for hiking, skiing and solace. By the nineteenth century, the first naturalists provided the more detailed observations of how the natural world changes with altitude (Lomolino 2001). In their first voyages around the world, they noted that the types of habitats and the number of species changed predictably with altitude. Several factors change predictably with increasing altitude; the most obvious being temperature, decreasing linearly approximately 0.6°C for each 100 m increase in altitude (Barry 1992). Tropical mountains, due to higher temperatures at low latitudes, have warmer temperatures at the base and therefore need to be much taller to reach the extreme cold temperatures seen on temperate mountains. Other abiotic factors that vary predictably with altitude are air pressure, which decreases with increasing altitude, and solar radiation, which increases with increasing altitude. Other climatic and abiotic factors vary along montane gradients but have a more complex relationship to altitude. Probably most important of such factors is precipitation, which is in the form of rain, snow and condensation from clouds. Tropical mountains show variable patterns, either with highest precipitation at middle altitudes or monotonously increasing precipitation with altitude. Some mountains show little variation in precipitation (Barry 1992). Most altitudinal gradients have a more or less stable condensation zone (cloud zone) at a certain level, especially conspicuous in the tropics, causing favourable conditions for certain taxa (e.g. epiphytes at mid-altitudes, which in turn create microhabitats and food for other taxa; Rahbek 1995).

Based on the first results from tropical regions in 1970s and 1980s, decreasing altitudinal diversity became the accepted and assumed pattern for all taxonomic groups for more than two decades (e.g. Brown and Lomolino 1998), and the unimodal altitudinal patterns observed by few naturalist were largely forgotten (McCain 2010). The uniformity of decreasing richness on altitudinal gradients was challenged by Rahbek (1995). Rahbek (1995) and later McCain (2007, 2009, 2010) described the main species richness patterns and presented series of studies showing possible causes.

Altitudinal patterns in species richness fall into four common patterns: decreasing, low plateau, low plateau with a mid-altitudinal peak and mid-altitudinal peak (Figure 2 in McCain 2009). Rahbek (1995) concluded that species richness patterns may differ between taxa as well as within taxa between different regions, and within the same region, at least on a regional scale.

Large number of hypotheses has been proposed to explain trends in species richness (Gaston 2000). Many of them are not mutually exclusive, while others hardly offer more substantial explanation. Some of them seem to have high explanatory power for plants, but lower for animals (Gaston 2000). While different taxa show various patterns based on their ecological requirements, one could expect the same to be true for different feeding guilds varying in their requirements and adaptations to habitats and climatic conditions. I therefore found of interest to examine the patterns of species richness of birds partitioned into trophically different groups.

Chapter **I** *deals with overall bird species diversity patterns along a complete altitudinal gradient in Central Range of Papua New Guinea, and focuses on the patterns of trophically different guilds (insectivores, herbivores and omnivores). Chapter* **II** *then reveals altitudinal range shifts and range extensions, and summarizes list of species for the region.*

Fragmentation in lowland areas

Extensive lowland regions represent second dominant feature of New Guinea. Fragmentation was a feature of lowland forests even before humans became a predominant influence. Semi-permanent open spaces resulted from the dynamic interactions of tree fall gaps provided by old aged trees, wind throw events, floods or landslides. Permanent open spaces in the woodland cover were maintained along river valleys, lakes, wetlands and cliffs (Dennis 1997).

Human influence has grown, and total forest cover declined during the last centuries in most of the areas of the world. Land use change and habitat fragmentation mainly caused by human activities exceeded natural limits. Population growth is often used as a proxy for land use change (Kok 2004). The New Guinea is not an exception; however the lowlands offer a different picture. The lowlands have the highest incidence of human malaria outside of Africa, and malaria is probably the main factor contributing to the low population density of ca 6 people/km^2 (Riley 1983). The New Guinea lowlands can thus be considered as ecologically marginal environment for human habitation lacking access to comparatively advanced technology, and this explains why they remain largely forested till today. The average size of traditional garden resembled in size the natural gaps caused by landslides and wind throws. The limited damage done by forest-dwelling populations to lowland forests also appears to be a consequence of technological impotence than of free choice.

The replacement of stone axes by steel ones, and these in turn by chainsaws, has finally provided the lowland communities with the efficiency to pursue the developmental trajectory already charted by their highland neighbours several thousand years ago. ‘There is little robust evidence that . . . ‘‘traditional’’ societies . . . have been natural conservationists. On the contrary, wherever people have had the tools, techniques, and opportunities to exploit natural systems they have done so’ (Oates 1999). Human population growth in Papua New Guinea is very fast [from 2.3 million people in 1975 to 5.2 million in 2000 and to 7.1 million in 2012, National Census Data, and Ningal *et al.* (2008)]. Since 85% of the population relies on subsistence agriculture, population growth affects agricultural land use. Most new agricultural land was taken from primary forest and the forest area decreased from 9.8 ha person^{-1} in 1975 to 4.4 ha person^{-1} in 2000.

Those activities turned the structure of Madang district lowland forest inside out – from the extensive cover of primary lowland forest with occasional small-scale gaps (natural or man made) into a large scale secondary growths and plantations with fragments of primary forest. The changes happening in Madang lowlands are rather fast. This fact could significantly influence the assemblages of organisms adapted to more certain natural conditions. For example in forests, some species prefer the open habitats created by the death of a tree or harvesting of trees, while the other avoid such habitats. Some authors believe that the organisms originating in areas with relatively low and small scale natural disturbance (which is the case for Madang lowlands) will be much strongly dependent on closed undisturbed habitats than the species form areas with severe and frequent habitat disturbances (e.g. hurricane disturbance in South America, not so recent large-scale gardening and logging; Pickett 1985).

Forest fragmentation affects the composition of forest bird communities, especially in the humid tropics where the rates of forest destruction are high and where birds are generally more specialized in their foraging tactics, live in more specific habitats, and need larger territories than in temperate forests (Stouffer and Bierregaard 1995, Hagan *et al.* 1996). Different bird species react differently to deforestation (Hagan *et al.* 1996) and forest understory insectivores, in general, have high habitat specificity, low mobility, and are more confined to forest interior than other forest passerine guilds, especially in the tropics where forest fragmentation and its consequences are most dramatic (Sekercioglu 2002, Sekercioglu *et al.* 2002). Other authors reported also large frugivores to be sensitive to habitat change (Lees and Peres 2010, Sekercioglu 2012).

Although over a dozen hypotheses have been proposed to explain the disappearance of insectivorous bird species from forested habitats around the world (Canaday 1996, Ford *et al.* 2001), four of these are particularly relevant: 1. The food scarcity hypothesis states that small fragments are impoverished in prey preferred by understory insectivores (Burke and Nol 1998, Zanette *et al.* 2000, Ford *et al.* 2001). 2. The microclimate hypothesis proposes that these birds are particularly sensitive physiologically to changes in microclimate associated with forest fragmentation (Karr and Freemark 1983, Canaday 1996). 3. The habitat specificity hypothesis states that the loss of some microhabitat elements (such as army ant swarms, curled leaves, and dead trees) from fragments may affect many understory insectivores negatively (Canaday 1996, Ford *et al.* 2001). 4. According to the limited dispersal hypothesis, understory insectivores may less likely disperse into more favourable habitats after forest fragmentation because of their relatively sedentary habits and possible psychological avoidance of clearings (Stouffer and Bierregaard 1995, Báldi 1996); and may therefore disappear from fragments as a result of stochastic events and other negative consequences of fragmentation.

In chapter **V**, *I deal with the effect of forest fragmentation on avifauna in lowlands of Papua New Guinea. I focus on patterns of trophically independent guilds (insectivores, frugivores and omnivores), and more intensively on insectivores which seems to be the most susceptible to habitat change (which can be seen also in chapter* ***I*** *and in Tvardikova 2010). In chapter* **VI**, *I discuss the predation pressure of insectivorous birds on herbivorous insect in different habitats in those lowland sites.*

Insectivorous birds

Why should be insectivorous birds different? The answer to this question seems to be compounded of several aspects. While the fruits and flowers can be carried on a plant in only limited number of ways, insect can conceal themselves or escape by a great variety of means. Diamond (1973) has shown that fruit-eating birds in south Pacific sort mainly by size, while, in contrast, it is routine to find several like-sized insectivores sharing the same habitat and segregating by subtle behavioural differences and searching techniques. The simple fact, that most avifaunas contain much larger numbers of insectivorous species and families, testify to the morphological specialization that can be effectively employed in pursuit of insect prey (Terborgh 1977).

Terborgh (1977) reported that tropical avifauna can be fairly discretely partitioned into three tropically distinct subdivisions: insectivores, frugivores (including granivores) and nectarivores, and that only minority of species feed on nearly equal mixtures of insect and fruits, or fruit and nectar. The opposite seems to be true, and many tropical species are reported to take much wider range of items. The question about the specialism, generalism or plasticity of food preferences were always of interest of avian ecologists. Many of them did not come with strong conclusions. Not only do species differ in their use of resources through time and in different places, but the extent to which they specialize or generalize in their use of resources may change. Often these changes are associated with seasonal or local patterns of prey abundance.

Some authors demonstrated that it was potentially misleading to characterize a species as either a foraging specialist or generalist without defining the resources being used, describing the spatial scale of the measurements made, and presenting some measure of the degree of individual variation within the population studied.

The diet of tropical bird species, including species in New Guinea, is particularly poorly known (Collins *et al.* 1990; Karr and Brawn 1990; Loiselle and Blake 1990). The feeding preference for most tropical bird species is usually inferred from a few individual observations; stomach contents of specimen collected for museums, or are totally unknown. Quantitative data on their diet are nevertheless important for the understanding of food webs in bird communities (Poulin *et al.* 1994a), and possible bird impact on their food (e.g. seed distribution) or prey (e.g. pest) regulation.

In chapters **III** *and* **V**, *I tried to identify food specialization of common bird species occurring in Papua New Guinea, and get better insight into their food preferences and food exploited in different habitats.*

Insectivorous birds as predators of arthropods

Insectivorous birds are common in ecosystems throughout the world, and numerous studies have shown that they can affect the population sizes of insects and other small arthropods (e.g. Holmes 1979; Fowler *et al.* 1991; Williams-Guillén *et al.* 2008). There is a direct conflict between the need of insectivorous birds to feed upon arthropods, and the need of arthropods to survive and feed themselves (mostly on plants). Arthropods therefore use a range of defences to protect themselves against attacks (e.g. Schmidt 1990), and birds try to overcome them.

When first confronted with the huge complexity and magnitude of tropical forest, I was wondering how the insectivorous birds deal with the primary condition of their survival – to find the food (i.e. arthropods) there. Having in mind the relative scarcity of arthropods in tropical forest, I was also interested in the chances of arthropod for their survival (or death in beaks of insectivorous birds). I experimentally studied those questions in chapters **IV** and **VI**.

Possible ways for birds to detect arthropods

The two primary sensory mechanisms that birds may use to detect plants carrying herbivores are vision and olfaction. One hypothesis is that vision can be important in detecting herbivores at both long and short distances, while use of olfaction may be useful mainly closer to the damaged plants, but the mechanism is not well known.

Visual

Birds can naturally use visible feeding marks in leaves or qualitative structural differences as cues to find arthropods (Heinrich & Collins 1983; Mols & Visser 2002; Boege & Marquis 2006; Müller *et al.* 2006; but see Bergelson & Lawton 1988), as most of the arthropods are herbivores. Also non-herbivore arthropods (e.g. spiders) are known to be attracted more to the leaves where the herbivory damage is going on, and they can find there more food for themselves, but also risk higher exposition to own predators. Visible marks of presence of arthropods could be herbivorous damage, excrements, or changes in leaf reflectance.

In addition to their broad range of vision (315 – 700 nm), diurnal birds can distinguish a large scale of chromatic variation; thus they see colours differently and with more shades than humans (Cuthill 2006). This is because birds have four cone cell types and colour-vision-enhancing oil droplets in their eyes, giving rise to a tetrachromatic form of vision in which every perceived colour consists of red, green, blue and ultraviolet (UV, 315 – 400 nm) components. In comparison, humans have only three cone cell types and trichromatic vision, lacking the UV part visible to birds (Cuthill 2006; Jones *et al.* 2007). The UV vision of birds may be a good candidate for the mechanism behind the attraction of birds to plants suffering from herbivore defoliation, as several bird species are known to use it for instance during foraging (e.g. Church *et al.* 1998; Honkavaara *et al.* 2002; Viitala *et al.* 1995). Additionally, insect herbivory induces the production of defence chemicals (Haukioja 2003), such as flavonoids, which are visible in UV wavelengths (Valkama *et al.* 2003).

Olfaction

In contrast to vision, the olfactory ability of most birds, including passerines, was long thought to be negligible (Roper 1999). Recent studies, however, have shown that passerines can make use of olfaction in many situations, such as in aromatising nests

(Petit *et al.* 2002; Mennerat *et al.* 2005; Gwinner & Berger 2008; Mennerat 2008) and in predator recognition (Amo *et al.* 2008; Roth *et al.* 2008). Many invertebrate predators in tritrophic systems use VOCs produced by plants to detect and locate their prey (Turlings *et al.* 1990; Dudareva *et al.* 2006). Novel VOCs emitted by herbivore-damaged plants may be the first indicators of herbivore presence to predators. It is therefore possible that olfaction may also be utilised by birds in receiving signals from plants. Physiological and genetic evidence confirm the olfaction ability of birds. Steiger *et al.* (2008) studied nine bird species (Blue Tit *Cyanistes caeruleus*, Black Coucal *Centropus grillii*, Brown Kiwi *Apteryx australis*, Canary *Serinus canaria*, Galah *Eolophus roseicapillus*, Red Junglefowl *Gallus gallus*, Kakapo *Strigops habroptilus*, Mallard *Anas platyrhynchos*, and Snow Petrel *Pagodroma nivea*) and found that they all had more active olfactory receptor genes than had previously been assumed. It thus seems that birds can detect smells much better than has previously been thought.

Aims of the thesis

In this thesis, I studied the factors driving distribution of birds across different habitats in Papua New Guinea. First, I focused on a complete forest altitudinal gradient, and aimed to describe patterns of bird species distribution, and further analyzed the factors driving them. I approached the question both for all bird species as well as different feeding guilds. Later, I focused on similar questions in forest fragments (and altered habitats in Tvardikova 2010) in lowlands of Papua New Guinea. In both cases, I found different patterns of diversity and abundance for insectivorous birds that for the other feeding guilds. Namely, insectivores were more sensitive to microhabitat, and changes in habitat structure. Therefore, I further focused on the insectivorous birds in more detail, and analyzed food specializations of the common species of the birds observed along altitudinal gradient and in forest fragments. My aim was to determine feeding specializations of birds more precisely, analyze the food preferences, find out the most important arthropods taken by insectivorous birds, and identify possible trend in food specialization which could help me to understand the patterns in diversity observed along altitudinal gradient. With the similar goal, I conducted predation experiments along altitudinal gradient, where I studied predation pressure from insectivorous birds (and other predators) on Lepidoptera larvae. In this experiment, I also studied whether passerine birds are attracted to herbivore-damaged trees, or whether leaf-rolling Lepidoptera larvae are better protected than free living individuals

MATERIALS AND METHODS

In this chapter, I briefly introduce the methods used in the studies included in the thesis (chapters **I – VI**). Overview of the methods used in individual studies is summarized in **Table 1**. More detailed accounts of the methods can be found in individual chapters.

All studies were carried out in Papua New Guinea. Studies **I – IV** were carried along rainforest altitudinal gradient on the slopes of Mt Wilhelm (4509 m asl) in the Central Range, spanning from the lowlands floodplains of the Ramu river (200 m asl, S5° 44' E145° 20') to the tree line (3700 m asl, S5° 47' E145° 03'). Studies **V** and **VI** were carried out mainly in lowland rainforest of Madang province, in continuous forest (Wanang 3 site), forest fragments of different size (Baiteta, Baitabag, Ohu sites), secondary forest (Wanang 1 site), and primary forest at the altitude of 1700 m asl was surveyed in study **V**.

Bird survey

Bird communities were surveyed by 3 types of censuses at all experimental sites – point counts, mist-netting and random walks through the area. Point counts were always carried out at 16 points regularly spaced along a 2250 m transect (successive points were 150 ± 5 m apart to avoid overlap). All birds seen or heard were recorded in the following radial distance classes in meters: 0 - 10, 11 - 20, 22 – 30, 31 – 40, and 41 – 50. Birds estimated to be beyond 50 m were not recorded for analyzes, but noted for complete checklists (chapter **II**). We started censuses 15 min before the day break (to standardize across altitudes, sites and seasons), at a randomly selected the starting point and the direction of walk. Each count lasted 15 minutes so that all 16 points were surveyed before 11 am.

Further, we mist-netted birds into 200 m long line of nets (using nets 2.5 m high x 12-18 m long, mesh 16 mm) from 5:30 am to 5:30 pm daily, with regular checks every 20 minutes. All mist-nets were moved to a new location (~300 m apart from first location) after every 3 days.

Finally, we randomly walked (2 km^{-h}) along point-count transects, and surrounded area and recorded all individual birds seen or heard within 50 meters radius.

Bird's food sampling

Food samples were obtained from mist-netted birds by administering tartar emetic following method by Poulin *et al.* (Poulin *et al.* 1994b; Poulin *et al.* 1994c; Poulin and Lefebvre 1995). Immediately after the capture, birds were given 0.8 cm^3 of 1.5%

antimony potassium tartar per 100g of body mass. I lowered the concentration from 1.5% to 1.0% for birds smaller than 10 g according to recommendations (Poulin and Lefebvre 1995). The solution was given orally through a flexible plastic tube attached to a 1-cc syringe. After administration, the birds were placed in a special “regurgit-bowl” covered by dark cloth. I examined each food sample (defined as regurgitated food of a single bird individual) under a dissecting scope. The number of arthropod individuals per morphospecies was assembled from body parts found in the sample. Most of the arthropods were fragmented, and their identification was thus based on the least digestible and most characteristic parts (guide available online http://tvardikova.weebly.com/downloads.html). Individual arthropods were identified to morphospecies (i.e. morphologically identical prey categories assumed to represent one species), and classified to orders or families where possible. Analyzes were also based on the classification of arthropods into the higher taxa listed in original articles.

Caterpillar experiments

I used artificial caterpillars exposed on the study trees to monitor attacks by natural enemies. Caterpillars were made from natural-looking dark green colour modelling clay (Koh-I-Noor Hardtmuth brand), which is malleable, oil-based and non-toxic. We modelled artificial caterpillars by pressing the plasticine through a syringe to ensure that each caterpillar had an absolutely smooth surface. Artificial caterpillars were 15 mm long and 3 mm in diameter, matching in body size locally common crambid and tortricid caterpillars, and also matching the median caterpillar size in the entire caterpillar community (Novotny and Basset 1999), as well as the size of caterpillar most commonly taken by birds. Each experiment was conducted along a single 2250 m long transect at each study site. Thirty sampling points, represented by individual trees, were spaced at approximately 75 m intervals along transect. This spacing ensured that the experimental trees could be considered independent. Artificial caterpillars were placed on each tree, between 2.5 and 4 m above the ground. They were pinned on the young leaves in various ways (see chapter **IV** and **VI** for more details). Each caterpillar was inspected at 24-h intervals for five (or six) consecutive days and carefully examined for characteristic bite marks (see Appendix 3 or http://tvardikova.weebly.com/downloads.html for identification guide). Missing caterpillars were excluded from the analyses as their status could not be ascertained. All missing caterpillars and caterpillars with marks of attack were replaced by new ones, pinned to approximately the same locations.

Arthropod survey

We sampled the arthropod communities from ten tree saplings at each site. Crowns of ten tree sampling (DBH ~5 cm) were lowered above mosquito net, covered by net and sprayed by commercial insecticide. All arthropods were collected and placed in 70% alcohol. Arthropods were further identified into orders, counted and measured into nearest 0.1 mm. All leaves were collected, weighted and leaf area was measured in leaf frames, and arthropod abundances were related to leaf area or leaf weight.

We surveyed ant communities occurring on experimental trees by observation and hand collection, as well as using tuna baits. Observation of ant activity was performed prior to the exposure of caterpillars. The trunk of each tree was examined for 10 minutes, all foraging ant individuals were counted and voucher specimens were taken for identification. Commercial canned tuna was used in baits, which is a standard method in the studies of foraging ant communities (Janda and Konečná 2011). One tea spoon of tuna was placed as bait under a stripe of gauze at breast height at each experimental tree. Baits were inspected one and three hours following their exposure. All ants present were counted and voucher specimens for each species were collected without disturbing the remaining ants.

Other arthropod data reported in studies were obtained by colleagues by various methods described in individual chapters.

Vegetation survey

At each point-count point, we measured the following variables according to methods in Bibby *et al.* (1992) (all estimates made by KT): shrub and canopy height (3 measures per point, using laser pointer); shrub density (using scatter plots, 5 measures per point); percentage of ground covered by grass, bare ground and litter (15 measures in 1x1 m square per point); percentage of point covered by shrub (5 measures per point); canopy openness (5 photos taken per point – analyzed in Gap Light Analyzer; Frazer 1999, Frazer *et al.* 2001). In each site, we had data loggers (Comet System) recording humidity and temperature every hour.

Study IV: In each site we conducted three 150 x 1 m lines (between points 3-4, 6-7, 12-13) where we counted all trees (DBH >1 cm), and categorized them into three size classes based on diameter at breast height (dbh): trees ≤ 7 cm, trees > 7–15 cm, and trees > 15 cm. We also categorized the leaf size of trees (as small, middle, large).

Study I: Botanical surveys were completed in three plots 20 x 20 meters at each altitude, and all plants (DBH > 5 cm) were tagged and identified by team of botanists (The New Guinea Binatang Research Center and PNG Forest Research Institute Lae)

Table 1. List of studies, sites where they were conducted, and survey methods and effort

Study	Sites	Bird survey effort			Methods used
		Point-Count	Mist-netting	Random walks	
I	8 sites along altitudinal gradient	14 replications	11 replications	20 hours	**Bird survey** **+ Vegetation survey**
II	8 sites along altitudinal gradient	14 replications	11 replications	20 hours	**Bird survey** **+ daily checklists of observed birds**
III	8 sites along altitudinal gradient, Wanang, Kotet	NA	11 replications	NA	**Bird's food sampling**
IV	8 sites along altitudinal gradient	14 replications	11 replications	20 hours	**Caterpillar experiments** + **Bird survey** + **Arthropod survey**
V	4 sites in lowlands = Wanang, Baiteta, Baitabag, Ohu	9 replications	6 replications	NA	**Bird survey** + **Arthropod survey** + **Bird's food sampling** **+ Vegetation survey**
VI	3 sites in lowlands and 1 at 1700m asl Wanang – primary, secondary, Ohu, Kotet	9 replications	6 replications	20 hours	**Caterpillar experiments** **+ Vegetation survey**

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Chapter I

Species richness of birds along a complete rainforest altitudinal gradient in the tropics

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(manuscript)

Species richness of birds along a complete rainforest altitudinal gradient in the tropics

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ABSTRACT

Aim We examine whether available area, regional species pool, mid-domain effect, contemporary climate, or habitat complexity determine species richness of birds along a complete, undisturbed forest altitudinal gradient in tropics. Further we investigate whether patterns of species richness of herbivores, insectivores, and omnivores are the same along the gradient.

Location Rainforest altitudinal gradient on the slopes of Mt. Wilhelm (4509 m a.s.l.) in the New Guinea Central Range, spanning from the lowlands floodplains of the Ramu river (200 m a.s.l., S5° 44’ E145° 20’) to the tree line (3700 m a.s.l., S5° 47’ E145° 03’).

Methods Data on bird communities were collected at eight sites during three independent surveys – in dry and wet seasons during two years. Birds were recorded by three standardized methods – point counts, mist-netting and random walks throughout a standardized area. Five predictors of diversity were tested, including all sets of their interactions. Habitat complexity (e.g. shrub density, tree height, plant richness) and contemporary climate (local temperature and humidity), were locally measured, area available at altitudinal belts was obtained using GIS software, regional species pool was determined from literature and mid-domain effect was simulated from empirical ranges.

Results Birds display monotonous decline in species richness with altitude. This decline is driven by herbivorous birds, whose species richness decreases steeply between 700 m and 1200 m a.s.l., while species richness of insectivorous birds exhibits a plateau from 200 to 1700 m a.s.l. The observed patterns of species richness were best explained by habitat complexity for all bird species and for insectivorous birds, whilst climate was best predictor for herbivorous birds.

Main conclusion The avian species richness corresponded well to climate, habitat complexity, and regional species pool. On the other hand, available area and mid-domain effect both represent sources of error rather than mechanisms underlying these avian diversity patterns.

Keywords
Avian, altitudinal gradient, diversity, humidity, temperature, species richness, climate, mid-domain effect, indirect effect, habitat complexity

INTRODUCTION

Altitudinal gradients provide striking patterns in diversity, an attractive setting for biodiversity studies, and serve as a heuristic tool and natural experiment in the study of community ecology (Lomolino, 2001; Rahbek, 2005; Nogués-Bravo *et al.*, 2008; Sanders & Rahbek, 2011). Virtually all plant and animal taxa respond to altitudinal gradients, but species richness patterns greatly vary among individual taxa, reflecting their ecology (Rahbek, 1995; Gaston, 2000). Many individual patterns have been variously defined and named but they cluster to four principal types: (i) declining species richness with altitude, (ii) a plateau at low altitudes (< 300 m a.s.l.) followed by decline, (iii) a plateau at low to middle altitudes followed by decline, and (iv) a mid-altitude peak in species richness (Rahbek, 1995; Rahbek, 1997; McCain, 2007; McCain, 2009; McCain, 2010). Rarely, species richness increases with altitude along complete gradients (e.g. for salamanders and lichens; Martin, 1958; Wake *et al.*, 1992; Grytnes *et al.*, 2006). Understanding such patterns and their underlying mechanisms is critically important for conservation efforts (Hunter & Yonzon, 1993), especially in montane regions which are likely to be especially threatened by climate change, and regions that have been generally un- or under-explored by biologists.

Large number of hypotheses has been proposed as determinants of species richness, and any of them are not mutually exclusive. Based on high correlations with species richness, contemporary climate and energy variables (e.g. precipitation, temperature and/or evapotranspiration) often explain spatial variation in species richness better than any other, non-climatic, variables (Hawkins *et al.*, 2003; Currie *et al.*, 2004; McCain, 2009). However, a number of other factors have been also correlated with observed patterns of species richness, including habitat complexity and foliage stratification (MacArthur & MacArthur, 1961), regional and evolutionary history (e.g. Rahbek & Graves, 2001; Jetz & Rahbek, 2002), regionally available area (Rahbek, 1997), regional species pool (Cornell & Lawton, 1992), mid-domain effect (Colwell & Lees, 2000) or even sampling effort (McCain, 2010).

The relationships between species richness and contemporary climate are less pronounced for animals than plants (Rahbek & Graves, 2001; Jetz & Rahbek, 2002).

Indirect effect of energy on animals through trophic interactions is a likely explanation, instead of direct physiological limitations. This assumes that species richness of animals is determined by the abundance, distribution and diversity of food resources, i.e. plant biomass for herbivores, fruits for frugivores (Kissling *et al.*, 2007), and various prey for carnivores. However, trophically and ecologically different species from the same taxon (e.g. carnivorous and herbivorous birds) are often combined together in studies on species richness along altitudinal gradients while their response to climate productivity or habitat characteristics could differ, obscuring thus the link between diversity and contemporary climate.

In this study, we examine bird species richness along one of the few complete rainforest undisturbed altitudinal gradients in the tropics, using constant sampling effort at all altitudes. Present data comes from Mt. Wilhelm altitudinal gradient in Papua New Guinea, a region surveyed poorly for birds in the past. We examine whether the observed species richness pattern could be determined by available area, regional species pool, mid-domain effect, contemporary climate, or habitat complexity. To disentangle the effect of these factors on bird species with different ecologies, we use species richness partitioned into three feeding guilds – insectivores, herbivores, and omnivores.

MATERIALS AND METHODS

Our study was performed on the slopes of Mt. Wilhelm (4509 m a.s.l.) in the Central Range of Papua New Guinea. The complete rainforest gradient spanned from the lowland floodplains of the Ramu river (200 m a.s.l., S5° 44’ E145° 20’) to the timberline (3700 m a.s.l., S5° 47’ E145° 03’; Fig. S1). The study was completed along a 60 km long transect with eight sites, evenly spaced at 500 m altitudinal increments. Average annual precipitation is 3288 mm (local meteorological station) in the lowlands, rising to 4400 mm at 3700 m a.s.l., with a distinct condensation zone around 2500 – 2700 m a.s.l.. Mean annual temperature decreases from 27.4°C at the lowland site to 8.37°C at the tree line at a constant rate of 0.54 °C per 100 altitudinal metres. Gradient doesn’t have any obvious ecotones, and the typical species composition of forest (Paijmans, 1976) and general climatic conditions (McAlpine *et al.*, 1983) are described elsewhere.

Bird sampling

Bird communities were surveyed by three methods at each altitudinal site – point counts, mist-netting and random walks through the area. Point counts (PC) were carried out at 16 points regularly spaced along a 2250 m transect (successive points were 150 ± 5 m apart to avoid overlap). All birds seen or heard within radial distance 0 - 50 m were recorded. Point counts started at 5:45 am, and lasted 15 minutes, so that all 16 points were surveyed before 11 am. We completed 1792 point counts representing 448 hours counts during entirety of this study. Further, we mist-netted (MN) birds into 200 m long line of nets (2.5 m high x 12-18 m long, mesh 16 mm) from 5:30 am to 5:30 pm daily. We identified all mist-netted individuals into species, marked them by color rings and released within 10 minutes. Finally, we randomly walked (RW, 2 km^{-h}) across the area (~80 ha), and continuously recorded all individual birds seen or heard within 50 meters radius. Random walks started at 3 pm and lasted till 5 - 6 pm, later standardized to 20 hours per site. All surveys were conducted by three observers (KT, BK, SJ), in three teams of two observers with rotating membership. We also recorded unclear voices during all surveys, for later identification. We adopted the species-level taxonomy of Handbook of the birds of the world (Hoyo *et al.*, 1992-2011).

The first survey was conducted between 9th April and 31th May 2010 (3 PC, 3 MN, 6 RW), the second between 26th July and 15th October 2010 (6 PC, 5 MN, 10 RW), and the third from 15th May to 15th July and from 1st August and 15th October 2012 (5 PC, 3 MN, 4 RW). In total, our data set for each site included 14 replications of point count surveys, 11 mist-netting days and 20 hours of random walks. Recorded birds were partitioned into three broad trophic guilds: insectivores, herbivores (granivores + frugivores) and omnivores (with equal intake of different items), based on dietary information in standard references (Peckover & Filewood, 1976; Beehler *et al.*, 1986; Hoyo *et al.*, 1992-2011), and our data. Only forest species were included in the analyses and all raptors and swifts were excluded (68 individuals of 15 species) since it was difficult to sample them in a standardized manner from within forest interior (Table S1 for list of species in analyzes and their feeding specialization).

Explanatory variables

We used surface area of altitudinal belts 200 m wide across the whole New Guinea mainland (e.g. 100 – 300 m a.s.l. for 200 m a.s.l. study site) as the proxy of available area. Surface area for each altitudinal site was measured in GIS software. Hypothetical regional species pool of birds (and birds partitioned according to feeding specialization) was determined from altitudinal distribution of all forest bird (excluding raptors and swifts similarly to local datasets) distributed across New Guinea mainland (using GBIF and New Guinea Birds database; and Hoyo *et al.* 1992-2011). Humidity and temperature were recorded every hour for the duration of one year (April 2010 – July 2011) by a data logger (Comet R3120) placed in forest interior at each site, and used as climatic variables. For habitat, we measured (i) canopy height (using laser pointer, 3 measures/point); (ii) shrub density (using scatter plots, 5 measures/point); percentage of ground covered by (iii) litter (15 measures in 1x1 m square per point); (iv) canopy openness (5 photos/point – analyzed in Gap Light Analyzer; Frazer, 1999; Frazer *et al.*, 2001) at each point. Botanical surveys were completed in three plots 20 x 20 meters at each altitude, and all plants (DBH > 5 cm) were tagged and identified by team of botanists (The New Guinea Binatang Research Center and PNG Forest Research Institute Lae). Botanical plots provided information about (v) tree genus richness, (vi) tree basal area, and (vii) tree density.

Hypotheses and testing

Area: Area of regional altitudinal belts (generally larger at lowland than at higher altitudes) can positively influence the number of species found there (Rahbek, 1997). Especially at the large spatial scales, the regional diversity along the regional altitudinal gradients may be highly influenced by area (i.e. direct effect of area - Rahbek, 1997; Brown, 2001; McCain, 2005), whereas area could have less influence on standardized sampling of local sites (i.e. indirect effect of area; Lomolino, 2001). On the other hand, Romdal & Grytnes (2007) found that the indirect area effect has also a considerable potential as basic influence of altitudinal diversity gradients. To test the indirect affect of surrounding area on the avian diversity, we predicted that the species richness increases according to the same species-area function across all altitudinal sites (Prediction I).

Species pool: A local community is inevitably assembled from a regional pool, and local richness may be directly proportional to regional richness, following a proportional-sampling model (Prediction I). Alternatively, as regional richness increases, local richness might attain a ceiling above which it does not rise despite continued increases in regional richness because of niche saturation (Gaston, 2000). The proportional relationships between local and regional richness would suggest the regional species pool as a prime driver of local richness while saturation model implies additional factors, limiting the number of coexisting species in highly diverse communities.

Mid-domain effect (MDE): The MDE assumes that spatial boundaries (e.g. the base and top of a mountain) cause higher overlap of species ranges toward the centre of an area where many large- to medium-sized ranges must overlap but are less likely to abut an edge of the area (Colwell *et al.*, 2004; Colwell *et al.*, 2005). On mountains, MDE predicts a unimodal diversity curve and maximal diversity at the mid-point of the mountain, and a strong, significant relationship between MDE fit and empirical species richness (Prediction I). Deviations in maximum diversity away from the mid-point of the mountain should be randomly distributed (Prediction II) if spatial constraints alone drive elevational diversity (e.g. effect of regional species pool, productivity or habitat heterogeneity is not directionally skewing the diversity peak away from the mid-point of the mountain).

Climate: Contemporary climate (or productivity) has been strongly and positively linked to diversity (Gaston, 2000; Kaspari *et al.*, 2000; Hawkins *et al.*, 2003). Productivity can be measured with numerous metrics. One group of metrics records the amount of solar energy, which is strongly positively correlated with temperature, radiation and potential evapotranspiration. The second type of metric measures actual evapotranspiration - the energy available for biota to convert into biomass, thus combining water and heat availability (Evans *et al.*, 2005). Species richness is predicted to be positively related to a combination of the warmest and wettest conditions (Prediction I). While temperature decreases with altitude on all mountains, rainfall and water availability follow more complex relationships with altitude depending on the local climate. On humid mountains like Mt. Wilhelm, water availability is high across a broad base of lower altitudes and only decreases toward the tops of the mountains, due to higher runoff. Therefore, bird species richness is predicted to exhibit decreasing or low-plateau pattern on wet mountains (Prediction II).

Habitat complexity (heterogeneity): The ‘habitat heterogeneity hypothesis’ is one of the classical diversity explanations (Simpson, 1949; MacArthur & Wilson, 1967). It assumes that structurally complex habitats provide more niches and ways of exploiting the environmental resources and thus increase species diversity. For example, for bird species diversity in forests, MacArthur (MacArthur & MacArthur, 1961; MacArthur *et al.*, 1962a) showed that the physical structure (foliage height stratification) of a plant community directly influences bird species richness. He suggested that each species requires a "patch" of vegetation with a particular forest stratum as its particular micro-habitat, and that the variety of "patches" of vegetation within a habitat determines the variety of bird species breeding there. If habitat complexity has power to determine species richness, a structurally complex habitats will have higher species richness, and habitat structure will have higher explanatory power than productivity itself (Prediction I and II). Especially for habitat sensitive insectivorous species (Prediction III; Robinson & Holmes, 1982) which are influenced by habitat complexity actually two times - directly via suitable living or nesting space and indirectly via arthropods, which feed on plants and represent food resource for birds.

In most habitats, plant communities determine the physical structure of the environment, and have therefore a considerable influence on the distributions and interactions of animals (Lawton, 1983; Bell *et al.*, 1991; McCoy & Bell, 1991). The assumption that the number of individual organisms increases with available energy and total biomass may not apply to plants, for which there is an evidence that as standing crop increases the numbers of adult individuals per unit area actually declines (and their size increases), which should tend to reduce species richness rather than increase it (Tilman & Pacala, 1993). Plant density and structure (i.e. growth form) therefore do not have to correspond to available energy. The scale of measurements also influences the resulting complexity. In large scales, lowland forest can be more structured, is higher and has lianas. In smaller scales, the mountain forest has many different epiphytes and mosses.

Statistical analyzes

Total number of species recorded at the standardized area and during the standardized time by all three survey methods was used in all analyzes. Most of the species was recorded during point-counts, while only few more species per site was recorded only by other survey methods (Fig. 1A).

All climatic and habitat predictor variables were subjected to principal component analysis (function princomp in R 2.15. software; R Core Team, 2012). For climatic model, the first axis corresponded to mean temperature, and second axis corresponded well to mean humidity, and all other measured variables (min, max temperature, and minimal humidity) were redundant (Table 1). For habitat complexity model, seven habitat variables (see *Explanatory environmental variables*) were subjected to principal component analysis. Tree fist axis corresponded to canopy height and to canopy openness, while the second axis corresponded to shrub density, and also to tree density (Table 1). Kaiser-Guttman stopping rule (Jackson, 1993) was used in both cases. Scores of the two axes were further used to predict the species richness for both models.

For mid-domain effect, we used RangeModel 5 (Colwell, 2008) to predict diversity based on Monte Carlo simulations and empirical diversity at each of sampled altitude (discrete domain analysis for empirical ranges and fills, eight domains and 500 replications). Poisson distribution with identity link function was used in models, and results were inspected for possible over dispersion with negative results. Area available in individual belts was log-transformed prior to analysis. Finally, we fitted individual regression models with all predictor variables (and their interactions) to empirical species richness. The same procedures were followed to analyze data partitioned to feeding specializations. We used Δ $\mathrm{AIC}_{c,}$ Akaike weights (w_i) and Evidence ratio (w_i /w_j) or R^2 to evaluate the models and their fits (Burnham & Anderson, 2002).

Table 1. Results of principal component analysis for climatic and habitat variables.

Climatic variables	Factor 1	Factor 2
Cumulative Proportion	0.654	0.928
Mean Temperature	-0.522	-0.237
Max Temperature	-0.437	-0.425
Min Temperature	-0.512	-0.206
Mean Humidity	-0.299	0.703
Min Humidity	-0.23	0.477
Habitat variables		
Cumulative Proportion	0.492	0.804
Tree Height	-0.957	-0.215
Canopy Openness	0.891	-0.232
Litter Cover	0.881	0.271
Genus richness	-0.815	0.486
Basal Area	-0.06	0.573
Tree Density	0.537	0.733
Shrub Density	0.259	0.888

RESULTS

Our data are based on observation of 33,639 bird individuals of 238 species (Table S1) recorded across eight altitudinal sites on the slope of Mt. Wilhelm. Altogether, 236 species and 25,240 individuals were recorded during point-counts, 1,354 individuals of 105 species were mist-netted, and 7,045 individuals of 200 species were observed during random walks (Fig. 1A). Insectivores were represented by 129 species, herbivores by 82 and omnivores by 27 species across the whole gradient.

Along the altitudinal gradients, the species richness of all birds decreased nearly linearly from 113 bird species recorded at 200 m a.s.l. to 37 bird species at tree line (Fig. 1A). The number of species in individual feeding guilds also decreased with altitude, but the patterns differed between guilds (Fig. 1B).

Our data show that the surface area available per altitudinal belt is positively correlated with species richness. However, fits of models were relatively poor (0.76 – 0.91) and ΔAICc scores higher than for the other models (Table 2).

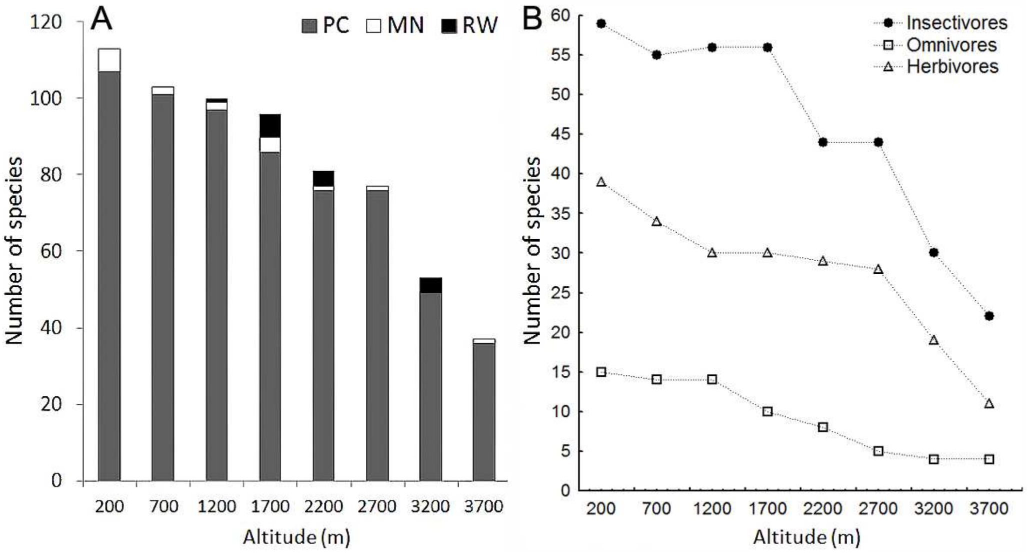

Figure 1. Species richness at altitudinal sites partitioned according to survey methods (A) and feeding guild (B). PC – point count (a priori selected as the main survey method, all species recorded by PC), MN – mist-netting (species recorded from nets but not PC), RW – random walks (birds observed during random walks but not PC or MN).

The local and regional species richness is positively correlated (according to prediction I) but not in directly proportional relationship. The models determine regional species pool as a very important factor influencing the local species richness but not as its main driver (Evidence ratio = 0.068; Table 1). Replacing total species richness in our models with data for guilds brought stronger support for regional pool as an important determinant of species diversity based on ΔAICc scores. Insectivores: evidence ratio = 0.35; Herbivores: evidence ratio = 0.87, Omnivores: evidence ratio = 0.98); however fits of models were poor (R^2 = 0.73 – 0.85) with comparison to other results (Table 2).

Observed bird species richness has very low concordance with the mid-domain effect predictions. Altitudinal species richness is not unimodal (contrary to prediction I), deviation of bird diversity are not randomly distributes around the mountain mid-point (contrary to prediction II), and the fits of models are poor in comparison with other tested models (<0.01 – 0.08, Table 1).

Table 2. Akaike's second-order information criterion (AICc) of the regression models of observed species richness at eight sites along altitudinal gradient, and the three combined models with the best ΔAICc scores. See Table S2 – S5 in Supplementary material for full set of interactions.

All birds (238 species)	Log-likelihood	R^2	Akaike weight (w_1)	AIC_c	ΔAIC_c
Habitat	1.00	0.98	0.27	63.33	0.00
Climate	0.90	0.95	0.24	63.54	0.21
Area	0.31	0.91	0.08	65.68	2.35
Species pool	0.07	0.85	0.02	68.69	5.36
MDE	0.00	0.05	0.00	117.29	53.96
MDE * Species pool	0.76	0.98	0.21	63.87	0.54
Species pool * Area	0.38	0.91	0.10	65.25	1.92
MDE * Area	0.18	0.95	0.05	66.76	3.43
Insectivores (129 species)					
Habitat	1.00	0.97	0.47	52.51	0.00
Area	0.53	0.86	0.25	53.78	1.27
Species pool	0.36	0.85	0.17	54.58	2.07
Climate	0.06	0.91	0.03	58.25	5.74
MDE	0.00	0.08	0.00	77.30	24.79
MDE * Species pool * Area	0.08	0.94	0.04	57.54	5.03
MDE * Area	0.08	0.94	0.04	57.58	5.07
Species pool * Area	0.03	0.87	0.02	59.23	6.72
Herbivores (82 species)					
Climate	1.00	0.98	0.23	52.69	0.00
Species pool	0.87	0.73	0.20	52.96	0.27
Area	0.52	0.81	0.12	54.01	1.32
Habitat	0.43	0.89	0.10	54.4	1.71
MDE	0.00	0.06	0.00	65.46	12.77
MDE * Species pool * Area	0.74	0.95	0.17	53.3	0.61
Species pool * Area	0.55	0.91	0.12	53.9	1.21
MDE * Area	0.27	0.83	0.06	55.32	2.63
Omnivores (27 species)					
Climate	1.00	0.92	0.18	48.44	0.00
Species pool	0.98	0.77	0.17	48.49	0.05
Habitat	0.87	0.92	0.15	48.72	0.28
Area	0.77	0.76	0.14	48.97	0.53
MDE	0.00	0.01	0.00	62.39	13.95
MDE * Area	0.78	0.91	0.14	48.93	0.49
Species pool * Area	0.59	0.88	0.11	49.48	1.04
MDE * Species pool * Area	0.57	0.88	0.10	49.56	1.12

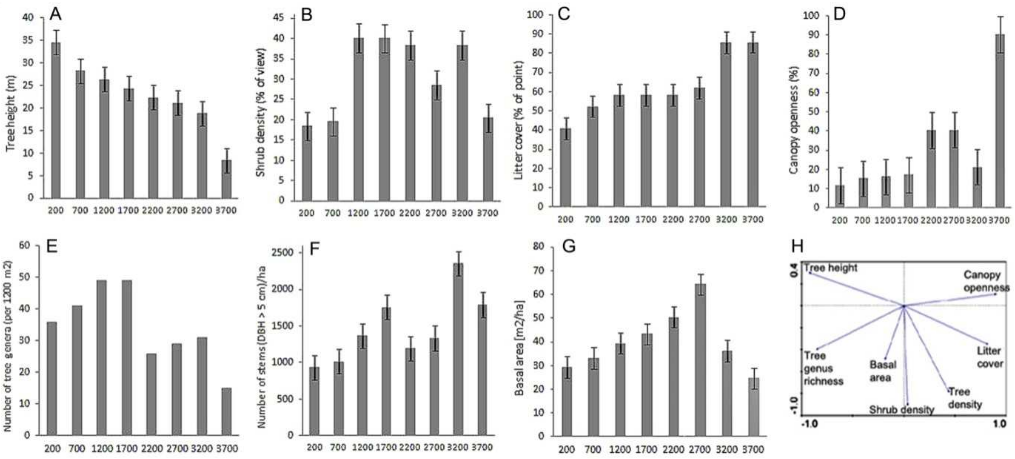

Figure 2. Habitat characteristics used in habitat model and the result of principal component analysis. A – tree height, B – vertical shrub density, C – percentage of ground of point covered by litter, D – canopy openness, E – number of tree genera per 1200 m2, F – number of tree (DBH > 5 cm) stems per ha, G – tree basal area [m2/ha], H – outcome of principal component analysis of habitat characteristics. Values in A-D, F and G are means + S.E..

Species richness is positively related to contemporary climate ($R^2 = 0.95$; Table 2) represented by local temperature and humidity (according to prediction I). Average temperature was more important component of the model than average humidity, while both of them were significant (Temperature: $t = 6.47$, $P < 0.001$; Humidity: $t = 2.87$, $P = 0.045$; according to prediction II). However, the fitted model underestimated observed species richness at mid-altitudes (1200 – 2200 m) and overestimated it at lowest altitude. Replacing total species richness with species richness partitioned between feeding specializations results in very different outcomes for each guild. While climate is one of the best determinant for herbivorous birds and omnivorous birds (together with regional species pool; Table 2), it gained only limited support for insectivorous birds (Evidence ratio = 0.05).

We find strong support for the effect of habitat complexity on insectivorous birds and also overall species richness (Table 2). Tree height and the shrub density are selected as the most important factors explaining 80% of variability of habitat characteristics (Table 2, Fig. 2). While tree height is the highest in low altitudes and decreases nearly linearly towards tree line, shrub density peaks in mid-altitudes (Table 1, Fig. 2), representing thus spatial forest complexity in vertical as well as horizontal space. Habitat complexity fitted model underestimated observed species richness only at 2200 m a.s.l., for both overall species richness and insectivores.

None of the multiple regressions combining explanatory variables explained substantially more variability than more simple models (Table S2 – S5). Only mid-domain effect in interaction with regional species pool could be considered as suitable determinant of local species richness (Table 2).

DISCUSSION

We observed a negative relationship between species richness of birds and altitude. Most importantly, we document that observed species richness is positively correlated and best fitted with habitat complexity. In agreement with many other studies, we showed that such species richness pattern correlates also with contemporary climatic conditions (McCain, 2007; McCain, 2009), and with regional species pool (Srivastava, 1999; Gaston, 2000) and available area.

Contemporary climate has been always strongly and positively linked to diversity (Gaston, 2000; Kaspari *et al.*, 2000; Hawkins *et al.*, 2003). Greater energy availability leads to greater biomass, which means more individual organisms, and thus more species able to coexist at abundance maintaining viable populations (Gaston, 2000). The result is an increase in species richness with energy availability. However, our data suggest that species richness responds to contemporary climate indirectly, via its effects on habitat complexity.

MacArthur (MacArthur & MacArthur, 1961; MacArthur *et al.*, 1962b) noted that a competent birdwatcher can look at a habitat and correctly name the bird species which will breed there in abundance. He 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 (Karr & Roth, 1971; Willson, 1974), but seems to be supported by our data from Mt. Wilhelm altitudinal gradient.

Habitat model fitted the empirical richness of all species and insectivorous birds much better than productivity. Horizontal (i.e. shrub and tree density) and vertical (i.e. tree height) stratification of habitat was particularly marked as the determinants of species richness. Lowland sites had very high and dense canopy layer, with low canopy openness, therefore lower stratification in forest interior and lower shrub density (Figure S2). Towards higher altitudes, the canopy was lower and more open, resulting in dense growth in forest understory, more epiphytes and distinct moss growth. The trees at uppermost altitudes were then very low, and most of the foliage was present in lower strata – in shrubs and especially in high grass. The fact that climatic model underestimates the species richness at altitudes, where shrub layer starts to be more pronounced (and tree basal area is the highest), shows that habitat complexity play important role for birds. Our data from insectivorous birds further support this presumption.

Insectivorous birds have been shown to be very sensitive to habitat structure (Sekercioglu, 2002) and changes in availability of microhabitat (Stratford & Stouffer, 2013). It is therefore not surprising that habitat complexity model gained in their case much stronger support than in the case of other birds. Forest structure significantly influence habitat selection of many bird species, and amount of understory foliage, canopy closure, and tree basal area are usually among the significantly important variables (Boves *et al.*, 2013). Our habitat model fitted all altitudes very well, except the site at 2200 m, where fitted values from habitat model were lower than already unexpectedly decreased bird species richness. This site was close to open areas around village Sinopass so that people could have disturbed the habitat by using the forest as the source of fire wood or building materials in the past (see also Fig. 2 for habitat characteristics of this site). Another explanation could be a natural dominance of *Pandanus* trees at that site, which have extremely low insect herbivore loads (pers. obs.) and as such seem to support fewer insectivorous birds also in other parts of New Guinea (Bell, 1969).

Insectivorous birds are likely to be influenced by habitat characteristics also indirectly via arthropods living and feeding on the foliage, and representing food resources for birds. Ghosh-Harir & Price (2013) found that the species richness of foliage gleaners along altitudinal gradient was limited by contemporary climate, through the available food resources. Other authors also documented altitudinal decrease in species richness of insectivorous birds due to disappearance of large insects (Schoener, 1971), or decreased range of arthropod body sizes (Orians, 1969). Insectivorous birds thus may be limited by either habitat complexity or food resources as indirect effects of contemporary climate.

Empirical data on richness of herbivorous birds were best fitted by climatic model, and habitat complexity did not seem to have strong effect. Their species richness decreased steeply between 200 to 1700 m a.s.l., then followed a plateau, and finally decreased very steeply from 2700 m a.s.l. towards the tree line. Species richness of frugivores is likely to increase with increasing range of fruit sizes and morphologies and/or with potentially higher production of fruit biomass (Ortiz-Pulido & Rico-Gray, 2000). Most herbivorous bird species do not specialize on the fruits (or seeds) of a particular plant species (Herrera, 1998; Zamora, 2000; Herrera, 2002). In contrast, some authors (Goodman & Ganzhorn, 1997; Kissling *et al.*, 2007) proposed a strong relationship between richness of *Ficus* trees and the entire guild of strict frugivores.

This could explain abrupt decrease in the number of herbivorous species above 2700 m a.s.l., coincident with *Ficus* altitudinal range limits between 2700 m and 3200 m on the slopes of Mt.Wilhelm. Abundances and species richness of *Ficus* species is decreasing towards 1200 m a.s.l. (Sam, L., unpubl. data), which could correlate with the steep decrease in species richness of frugivorous birds along our gradient. Most of the bird species restricted to lowlands (200 m a.s.l.) were large-bodied pigeons, doves and megapodes, which corresponds to the distribution of extremely large fruits, also restricted to lowlands (Duivenvoorden *et al.*, 2012). Alternately, large lowland areas can provide food resources for herbivorous birds, which are usually good migrants following abundant resources across large areas (Loiselle & Blake, 1991). We suggest that food resources, controlled by climate, have strong effect on herbivorous birds rather than habitat complexity.

The lowland forest covers the largest area of mainland (67% of area is below 500 m a.s.l.) in New Guinea, while the species richness gradient did not show such pattern and species richness decrease much slowly towards the higher altitudes. The indirect effect of area on altitudinal transects was, to our knowledge, first discussed by Beehler (Beehler, 1981), who found that a linear decrease in New Guinean forest birds on an altitudinal transect was paralleled by a decrease in regional area. Similarly, we found a strong, but not perfect, correlation between area and local species richness, pointing out the importance of other factors. Previous studies also found an indirect effect of area on specie richness of birds (Romdal & Grytnes, 2007), which can be lower in tropical areas with high available energy (Storch *et al.*, 2005) and in large forest areas (Romdal & Grytnes, 2007).

All local communities derive from regional species pools, which are thus logical candidates as determinants of these communities. However, several authors pointed out pitfalls in the interpretation on relationships between species pools and communities (Srivastava, 1999; Gaston & Blackburn, 2000). In particular, regional species pools should only include species capable of living in the studied habitats (as was done in the present study). Further, Loreau (2000) and Ricklefs (2000) pointed out that the relationship between local and regional species richness depends on the scale. The `regional' should be defined on a significantly large scale than “local” so that a large proportion of the regional heterogeneity is not sampled within a single site. Further, a narrow definition of `local' makes it independent of regional diversity but also more likely to include species saturation. The regional species pool has variously been defined by a geographic region, or as a pool of species that are capable of colonizing a particular site. We decided to include all birds occurring on the mainland of New Guinea within a particular altitudinal range as a regional pool, based on the knowledge of species distribution and history of the region (Norman *et al.*, 2007; Jønsson *et al.*, 2011). Our decision was made simple by the fact that the island of New Guinea represents a natural biogeographic unit.

Both proportional and dis-proportional sampling by local communities from regional pools has been reported (Cornell & Lawton, 1992; Gaston, 2000). In the case of our altitudinal gradient, a disproportional sampling was found (Type II response, Gaston, 2000) and we sampled 46.8 – 49.7 % of regional avifauna at altitudes 200 – 1200 m, and then the proportion of sampling steeply increased from 61.5 to 100 % of regional species richness.

The altitudinal ranges of species along the gradient are constrained physically by the lowest available altitude and the top of a mountain. Colwell and Lees (2000) suggested that MDE could be treated as a null model for gradients in species richness, assuming that species' geographic ranges are randomly placed over the domain in the absence of environmental gradients. These spatial constraints have been shown in some cases as a contributing factor to mid-elevational peaks in species richness (e.g. Colwell et al., 2004, 2005; but see Hawkins et al., 2005; Zapata et al., 2005). In the case of our gradient, none of the predictions of MDE were supported. Therefore we conclude that other environmental determinants are present and cause the observed pattern in species richness. The length of our gradient can also decrease the effect of spatial constraints as only small proportion of birds is able to occupy whole altitudinal gradient.

Eastern slope of Mt Wilhelm represents wet tropical montane habitat, thus the pattern of decreasing species richness was consistent with those found in other studies on birds in wet tropics (Kikkawa & Williams, 1971; Diamond, 1972; Terborgh, 1977a; Terborgh, 1977b; Goerck, 1999; Grytnes & Vetaas, 2002). In contrast to other studies, we were not able to identify climatic variables as main direct drivers of species richness. The present study rather supports indirect effect of climate via habitat structure or possibly via food webs. In particular, habitat complexity played an important role in shaping of local bird species richness.

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SUPPLEMENTARY MATERIAL:

Table S1. List of species recorded during standardized survey at eight altitudinal sites of Mt. Wilhelm gradient.

Figure S1. Location of the study sites in Papua New Guinea

Table S2. Akaike's second-order information criterion (AIC_c) of the regression models for total bird species richness across eight sites along altitudinal gradient, and their combinations.

Table S3. Akaike's second-order information criterion (AIC_c) of the regression models for species richness of insectivorous bird across eight sites along altitudinal gradient, and their combinations.

Table S4. Akaike's second-order information criterion (AIC_c) of the regression models of species richness of frugivorous birds across eight sites along altitudinal gradient, and their combinations.

Table S5. Akaike's second-order information criterion (AIC_c) of the regression models of species richness of omnivorous bird across eight sites along altitudinal gradient, and their combinations.

Figure S2. Forest interior and canopy openness at altitudinal sites.

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SUPPLEMENTARY MATERIAL

Table S1. List of species recorded during standardized survey at eight altitudinal sites of Mt. Wilhelm gradient. Guild: IN – insectivore, HE – herbivore, OM – omnivore, Food: In – insect, Ne – nectar, Fr – fruit, Ca – vertebrates, Gr – grains/seeds.

Scientific name	GUILD	Food		Altitude (m)							
		Primary	Secondary	200	700	1200	1700	2200	2700	3200	3700
Acanthiza murina	IN	In	Ne						X	X	X
Aegotheles albertisi	IN	In						X			
Aepypodius arfakianus	HE	Fr					X				
Ailuroedus buccoides	OM	Fr	In	X	X	X	X				
Ailuroedus melanotis	OM	Fr	In					X			
Alcedo azurea	IN	In	Ve	X	X	X					
Alcedo pusilla	IN	In	Ve	X							
Aleadryas rufinucha	IN	In					X	X	X	X	X
Alisterus chloropterus	HE	Fr			X	X	X	X	X		
Amalocichla incerta	IN	In					X				
Amblyornis macgregoriae	HE	Fr						X	X	X	
Anthus gutturalis	IN	In								X	X
Aplonis cantoroides	OM	Fr	In	X							
Aplonis metallica	OM	Fr	In	X	X						
Arses insularis	IN	In		X	X	X	X				
Artamus maximus	IN	In							X	X	X
Astrapia stephaniae	HE	Fr							X	X	X
Cacatua galerita	HE	Fr		X	X	X					
Cacomantis castaneiventris	IN	In		X	X	X	X	X	X		
Cacomantis flabelliformis	IN	In				X	X	X	X	X	X
Cacomantis variolosus	IN	In		X	X	X	X				
Caliechthrus leucolophus	IN	In		X	X	X					
Campochaera sloetii	OM	Fr	In	X		X					
Caprimulgus macrurus	IN	In		X							
Casuarius bennetti	HE	Fr							X		
Centropus phasianinus	IN	In	Ve	X	X						
Ceyx lepidus	IN	In		X	X	X					
Chaetorhynchus papuensis	IN	In		X	X	X	X				
Chalcophaps indica	HE	Fr		X	X						
Chalcophaps stephani	HE	Fr		X	X	X					
Charmosyna papou	HE	Fr	Ne				X	X	X	X	X
Charmosyna placentis	HE	Ne	Fr	X	X						
Charmosyna rubronotata	HE	Ne	Fr	X	X						
Charmosyna wilhelminae	HE	Fr			X	X					
Chlamydera lauterbachi	OM	Fr	In					X			
Chrysococcyx minutillus	IN	In		X							
Chrysococcyx ruficollis	IN	In							X	X	
Cicinnurus regius	OM	Fr	In	X	X						
Cinnyris jugularis	OM	Ne	In	X	X	X	X				
Clytoceyx rex	IN	In								X	X
Clytomyias insignis	IN	In					X	X			
Cnemophilus loriae	HE	Fr					X	X	X	X	
Cnemophilus macgregorii	HE	Fr						X	X	X	X
Colluricincla megarhyncha	IN	In		X	X	X	X	X			
Columba vitiensis	HE	Fr						X	X		

Coracina boyeri	OM	Fr	In	X	X	X					
Coracina caeruleogrisea	IN	In			X	X	X	X	X		
Coracina incerta	IN	In		X	X						
Coracina longicauda	IN	In							X		
Coracina melas	IN	In		X							
Coracina montana	OM	Fr	In			X	X	X	X		
Coracina papuensis	IN	In		X	X	X	X				
Coracina schisticeps	OM	Fr	In				X	X			
Coracina tenuirostris	IN	In		X	X	X					
Corvus tristis	HE	Fr		X	X	X	X				
Cracticus cassicus	IN	In	Ve	X	X						
Cracticus quoyi	IN	In		X							
Crateroscelis murina	IN	In		X	X	X	X				
Crateroscelis nigrorufa	IN	In					X				
Crateroscelis robusta	IN	In			X	X	X	X	X	X	X
Cyclopsitta diophthalma	HE	Fr	Ne	X	X	X	X				
Cyclopsitta gulielmitertii	HE	Fr		X							
Dacelo gaudichaud	IN	In	Ve	X	X						
Daphoenositta miranda	IN	In							X	X	X
Dicaeum geelvinkianum	HE	Fr	Ne	X	X	X	X	X			
Dicrurus bracteatus	IN	In		X	X						
Diphyllodes magnificus	HE	Fr			X	X	X				
Ducula chalconota	HE	Fr					X	X	X		
Ducula pinon	HE	Fr		X							
Ducula rufigaster	HE	Fr		X							
Ducula zoeae	HE	Fr		X	X	X					
Eclectus roratus	HE	Fr	In	X	X	X	X				
Epimachus fastuosus	HE	Fr				X	X	X	X	X	
Epimachus meyeri	HE	Fr					X	X	X	X	
Erythrura trichroa	HE	Fr					X	X	X	X	X
Euaegotheles insignis	IN	In							X		
Eudynamys scolopaceus	IN	In		X	X						
Eugerygone rubra	IN	In					X	X	X	X	X
Eulacestoma nigropectus	IN	In							X		
Eurystomus orientalis	IN	In		X	X						
Gallicolumba beccarii	HE	Fr				X	X				
Gallicolumba jobiensis	HE	Fr						X			
Garritornis isidorei	IN	In		X							
Geoffroyus geoffroyi	HE	Fr	Ne	X							
Geoffroyus simplex	HE	Fr	Ne	X							
Gerygone chloronota	IN	In		X	X	X					
Gerygone chrysogaster	IN	In		X	X						
Gerygone cinerea	IN	In					X	X	X	X	
Gerygone palpebrosa	IN	In		X		X					
Gerygone ruficollis	IN	In					X	X	X	X	X
Grallina bruijni	IN	In				X					
Gymnophaps albertisii	HE	Fr					X	X	X	X	X
Henicophaps albifrons	HE	Fr		X	X	X					
Ifrita kowaldi	IN	In					X	X	X	X	X
Lalage atrovirens	OM	Fr	In	X							
Leptocoma sericea	OM	Ne	In	X	X	X					
Lichenostomus obscurus	OM	Ne	In			X					
Lichenostomus subfrenatus	OM	Ne	In				X	X	X	X	X
Loboparadisea sericea	HE	Fr					X				

Lonchura spectabilis	HE	Gr						X			
Lonchura tristissima	HE	Gr		X							
Lophorina superba	HE	Fr					X				
Loriculus aurantiifrons	HE	Ne	Fr	X							
Lorius lory	HE	Fr	Ne	X	X	X					
Machaerirhynchus flaviventer	IN	In		X	X	X					
Machaerirhynchus nigripectus	IN	In					X	X	X	X	
Macropygia amboinensis	HE	Fr		X	X	X	X	X			
Macropygia nigrirostris	HE	Fr							X		
Malurus alboscapulatus	IN	In					X	X			
Manucodia chalybatus	HE	Fr			X	X					
Megapodius decollates	HE	Fr		X	X						
Melampitta lugubris	IN	In							X	X	X
Melanocharis longicauda	HE	Fr					X				
Melanocharis nigra	OM	Fr	In	X	X	X	X	X			
Melanocharis striativentris	HE	Fr					X		X		
Melanocharis versteri	OM	Fr	In				X	X	X	X	X
Melidectes belfordi	IN	In	Fr					X	X	X	X
Melidectes fuscus	IN	In						X	X	X	X
Melidectes princeps	OM	Ne	In							X	X
Melidectes rufocrissalis	IN	In	Ne				X				
Melidectes torquatus	IN	In	Ne			X	X	X			
Melidora macrorrhina	IN	In	Ve	X	X						
Melilestes megarhynchus	IN	In	Ne	X	X	X	X	X			
Meliphaga analoga	IN	In	Fr	X	X	X	X				
Meliphaga aruensis	IN	In	Fr	X	X	X					
Meliphaga montana	OM	Fr	In		X	X					
Meliphaga orientalis	IN	In	Ne				X	X	X		
Melipotes fumigatus	IN	In				X	X	X	X	X	X
Merops ornatus	IN	In		X	X						
Microdynamis parva	HE	Fr		X							
Microeca flavovirescens	IN	In		X	X	X					
Microeca griseoceps	IN	In				X					
Microeca papuana	IN	In					X	X	X	X	
Micropsitta bruijnii	HE	Ne	Fr		X	X					
Micropsitta pusio	HE	Fr	Ne	X	X						
Mino anais	HE	Fr		X	X						
Mino dumontii	OM	Fr	In	X	X						
Monachella muelleriana	IN	In		X							
Monarcha axillaris	IN	In				X	X	X	X		
Monarcha chrysomela	IN	In		X	X	X					
Monarcha frater	IN	In		X	X	X					
Monarcha guttula	IN	In		X	X	X					
Monarcha manadensis	IN	In		X							
Monarcha rubiensis	IN	In		X							
Myiagra alecto	IN	In	Fr	X	X	X	X				
Myzomela rosenbergii	OM	Ne	In			X	X	X	X	X	X
Neopsittacus musschenbroekii	HE	Fr	Ne			X	X	X	X	X	
Neopsittacus pullicauda	HE	Ne	Fr				X	X	X	X	X
Oedistoma iliolophus	OM	In	Ne		X	X	X				
Oreocharis arfaki	HE	Fr					X	X	X	X	X
Oreopsittacus arfaki	HE	Ne	Fr					X	X	X	X
Oreostruthus fuliginosus	HE	Gr									X

Oriolus szalayi	OM	Fr	In	X	X						
Otidiphaps nobilis	HE	Fr	In			X					
Pachycare flavogriseum	IN	In				X	X	X			
Pachycephala hyperythra	IN	In		X	X	X	X				
Pachycephala modesta	IN	In							X	X	
Pachycephala schlegelii	IN	In					X	X	X	X	X
Pachycephala simplex	IN	In			X	X					
Pachycephala soror	IN	In				X	X	X			
Pachycephalopsis poliosoma	IN	In				X	X				
Paradisaea minor	OM	Fr	In	X	X	X					
Paramythia montium	HE	Fr							X	X	X
Peltops blainvillii	IN	In		X	X						
Peltops montanus	IN	In					X	X	X		
Peneothello bimaculata	IN	In			X	X	X				
Peneothello cyanus	IN	In					X	X	X		
Peneothello sigillata	IN	In	Fr						X	X	X
Philemon buceroides	HE	Ne	Fr	X	X						
Philemon meyeri	HE	Fr	Ne	X	X	X					
Phylloscopus poliocephalus	IN	In				X	X	X			
Pitohui cristatus	IN	In				X					
Pitohui dichrous	IN	Fr	In		X	X	X				
Pitohui ferrugineus	IN	In	Fr	X							
Pitohui kirhocephalus	IN	In	Fr	X	X	X					
Pitta erythrogaster	IN	In		X	X						
Pitta sordida	IN	In		X	X						
Podargus ocellatus	IN	In				X	X	X			
Poecilodryas albispecularis	IN	In					X	X	X		
Poecilodryas albonotata	IN	In						X	X	X	
Poecilodryas hypoleuca	IN	In		X	X	X					
Probosciger aterrimus	HE	Fr		X	X	X					
Pseudeos fuscata	HE	Fr		X			X	X	X		
Psittacella brehmii	HE	Fr	Gr					X	X		
Psittacella picta	HE	Fr	Fr						X	X	X
Psittaculirostris edwardsii	HE	Fr	Ne	X	X	X					
Psitteuteles goldiei	HE	Ne	Fr						X	X	
Psittrichas fulgidus	HE	Fr						X			
Pteridophora alberti	OM	Fr	In						X		
Ptilinopus coronulatus	HE	Fr		X	X	X	X				
Ptilinopus iozonus	HE	Fr		X							
Ptilinopus magnificus	IN	Fr		X	X	X					
Ptilinopus ornatus	HE	Fr						X			
Ptilinopus perlatus	HE	Fr		X	X						
Ptilinopus pulchellus	HE	Fr		X	X	X					
Ptilinopus rivoli	IN	Fr					X	X	X	X	
Ptilinopus superbus	IN	Fr		X	X	X		X			
Ptiloprora guisei	HE	Fr					X	X	X	X	
Ptiloprora perstriata	IN	In	Fr					X	X	X	X
Ptiloris magnificus	HE	Fr	In		X	X					
Ptilorrhoa caerulescens	HE	In		X	X	X					
Ptilorrhoa castanonota	HE	In				X					
Ptilorrhoa leucosticta	HE	In					X	X	X		
Pycnopygius ixoides	OM	Fr	In	X	X	X					
Rallina forbesi	IN	In	Fr					X	X	X	
Reinwardtoena reinwardtii	HE	Fr		X	X	X	X	X	X	X	

Rhagologus leucostigma	HE	Fr					X	X	X		
Rhipidura albolimbata	IN	In					X	X	X	X	X
Rhipidura atra	IN	In		X	X	X	X	X	X		
Rhipidura brachyrhyncha	IN	In					X	X	X	X	X
Rhipidura leucothorax	IN	In		X	X	X					
Rhipidura rufidorsa	IN	In		X	X						
Rhipidura rufiventris	IN	In		X	X	X	X				
Rhipidura threnothorax	IN	In		X	X	X					
Rhyticeros plicatus	HE	Fr		X	X	X					
Saxicola caprata	IN	In						X			
Scolopax rosenbergii	IN	In							X		
Scythrops novaehollandiae	HE	Fr		X							
Sericornis arfakianus	IN	In				X	X				
Sericornis nouhuysi	IN	In					X	X	X	X	X
Sericornis papuensis	IN	In					X	X	X	X	
Sericornis perspicillatus	IN	In					X	X	X		
Sericornis spilodera	IN	In			X	X					
Syma megarhyncha	IN	In	Ve			X	X	X	X		
Syma torotoro	IN	In		X	X						
Talegalla jobiensis	OM	Fr	In	X	X	X	X				
Tanysiptera galatea	IN	In		X	X						
Timeliopsis fulvigula	IN	In					X				
Todiramphus macleayii	IN	In					X				
Toxorhamphus novaeguineae	IN	In	Ne	X	X	X					
Toxorhamphus poliopterus	IN	In	Ne			X	X	X			
Tregellasia leucops	IN	In	Fr	X	X	X	X				
Trichoglossus haematodus	HE	Ne	Fr	X	X	X					
Trugon terrestris	HE	Fr					X	X			
Turdus poliocephalus	IN	In							X	X	X
Xanthotis flaviventer	IN	In	Ne		X	X					
Zosterops minor	IN	In	Fr	X	X	X					
Zosterops novaeguineae	IN	In	Fr				X	X	X		
Total				113	103	100	96	81	77	53	37

Figure S1. Location of the study sites in Papua New Guinea (insert). Red dots denote study sites. Map courtesy of P. Shearman & J. Bryan, UPNG Remote Sensing Centre, Papua New Guinea.

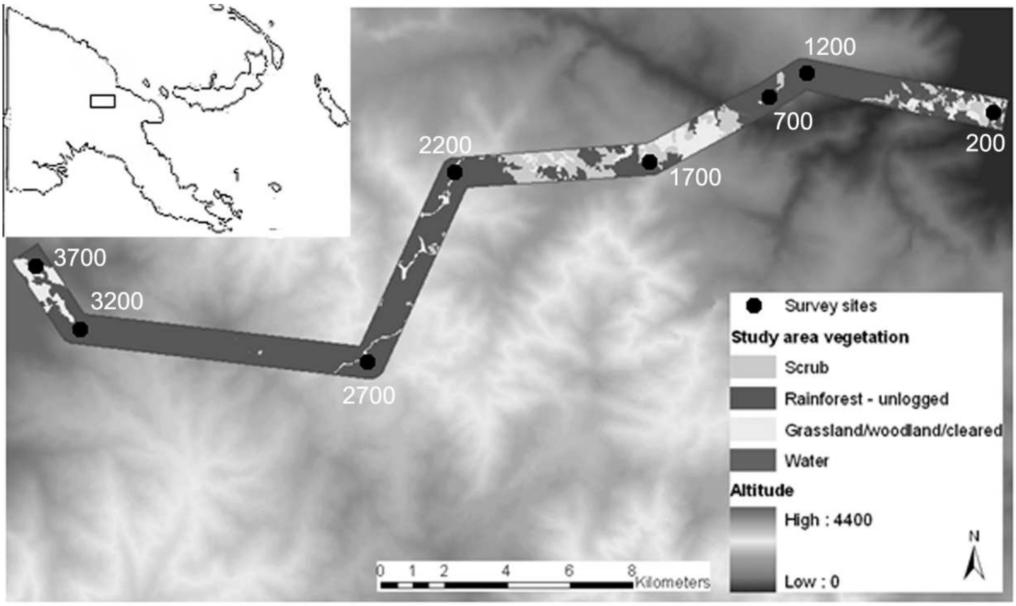


Table S2. Akaike's second-order information criterion (AICc) of the regression models for total bird species richness across eight sites along altitudinal gradient, and their combinations. Models sorted according to ΔAICc.

All birds (238 species)	Log-likelihood	R^2	Akaike weight (w_1)	AIC_c	ΔAIC_c
Habitat	1.00	0.98	0.27	63.33	0.00
Climate	0.90	0.95	0.24	63.54	0.21
MDE * Species pool	0.76	0.98	0.21	63.87	0.54
Species pool * Area	0.38	0.91	0.10	65.25	1.92
Area	0.31	0.91	0.08	65.68	2.35
MDE * Area	0.18	0.95	0.05	66.76	3.43
Species pool	0.07	0.85	0.02	68.69	5.36
MDE * Species pool * Area	0.02	0.98	0.00	71.34	8.01
Climate * Species pool	0.01	0.97	0.00	71.90	8.57
Habitat * MDE	0.01	0.99	0.00	72.13	8.80
Habitat * Area	0.01	0.97	0.00	72.43	9.10
Climate * MDE	0.01	0.95	0.00	72.61	9.28
Climate * Area	0.01	0.94	0.00	72.65	9.32
Habitat * Species pool	0.01	0.98	0.00	72.87	9.54
Climate * Species pool * MDE	0.00	0.99	0.00	89.97	26.64
Climate * Species pool * Area	0.00	0.99	0.00	90.20	26.87
Area * MDE * Habitat	0.00	0.98	0.00	90.29	26.96
Climate * Habitat	0.00	0.98	0.00	90.48	27.15
Climate * Area * MDE	0.00	0.96	0.00	90.63	27.30
Habitat * Species pool * MDE	0.00	0.99	0.00	90.64	27.31
Habitat * Species pool * Area	0.00	0.97	0.00	91.09	27.76
MDE	0.00	0.05	0.00	117.29	53.96
Habitat * Species pool * Climate	0.00	0.97	0.00	145.89	82.56
Climate * Species pool * MDE * Area	0.00	0.99	0.00	145.94	82.61
Habitat * Species pool * MDE * Area	0.00	0.98	0.00	145.99	82.66
Climate * MDE * Habitat	0.00	0.98	0.00	146.36	83.03
Climate * Habitat * Area	0.00	0.98	0.00	146.44	83.11
Habitat * Species pool * Climate * MDE	0.00	0.99	0.00	Inf	Inf
Climate * Habitat * MDE * Area	0.00	0.98	0.00	Inf	Inf
Climate * Habitat * Species pool * Area	0.00	0.99	0.00	Inf	Inf
Habitat * Species * Climate * MDE * Area	0.00	1.00	0.00	Inf	Inf

Table S3. Akaike's second-order information criterion (AICc) of the regression models for species richness of insectivorous bird across eight sites along altitudinal gradient, and their combinations. Sorted according to ΔAICc.

Insectivores (129 species)	Log-likelihood	R^2	Akaike weight (w_1)	AIC_c	ΔAIC_c
Habitat	1.00	0.97	0.47	52.51	0.00
Area	0.53	0.86	0.25	53.78	1.27
Species pool	0.36	0.85	0.17	54.58	2.07
MDE * Species pool * Area	0.08	0.94	0.04	57.54	5.03
MDE * Area	0.08	0.94	0.04	57.58	5.07
Climate	0.06	0.91	0.03	58.25	5.74
Species pool * Area	0.03	0.87	0.02	59.23	6.72
Habitat * Species * Climate * MDE * Area	0.00	0.96	0.00	66.49	13.98
MDE * Species pool	0.00	0.96	0.00	66.51	14.00
Habitat * Species pool * MDE * Area	0.00	0.96	0.00	66.62	14.11
Habitat * Area	0.00	0.95	0.00	66.76	14.25
Climate * MDE * Habitat	0.00	0.93	0.00	67.16	14.65
Climate * Habitat * Species pool * Area	0.00	0.92	0.00	67.39	14.88
Climate * Species pool * MDE * Area	0.00	0.91	0.00	67.58	15.07
MDE	0.00	0.08	0.00	77.30	24.79
Habitat * Species pool * MDE	0.00	0.98	0.00	84.73	32.22
Habitat * Species pool * Climate	0.00	0.96	0.00	85.04	32.53
Climate * Area	0.00	0.97	0.00	85.07	32.56
Climate * Area * MDE	0.00	0.96	0.00	85.15	32.64
Area * MDE * Habitat	0.00	0.96	0.00	85.17	32.66
Climate * Species pool	0.00	0.95	0.00	85.30	32.79
Climate * Species pool * MDE	0.00	0.93	0.00	85.68	33.17
Habitat * Species pool	0.00	0.99	0.00	140.40	87.89
Habitat * Species pool * Climate * MDE	0.00	0.98	0.00	140.55	88.04
Climate * Species pool * Area	0.00	0.97	0.00	140.87	88.36
Climate * Habitat * MDE * Area	0.00	0.97	0.00	141.14	88.63
Climate * MDE	0.00	0.96	0.00	141.15	88.64
Climate * Habitat	0.00	0.97	0.00	Inf	Inf
Climate * Habitat * Area	0.00	0.99	0.00	Inf	Inf
Habitat * MDE	0.00	1.00	0.00	Inf	Inf
Habitat * Species pool * Area	0.00	0.99	0.00	Inf	Inf

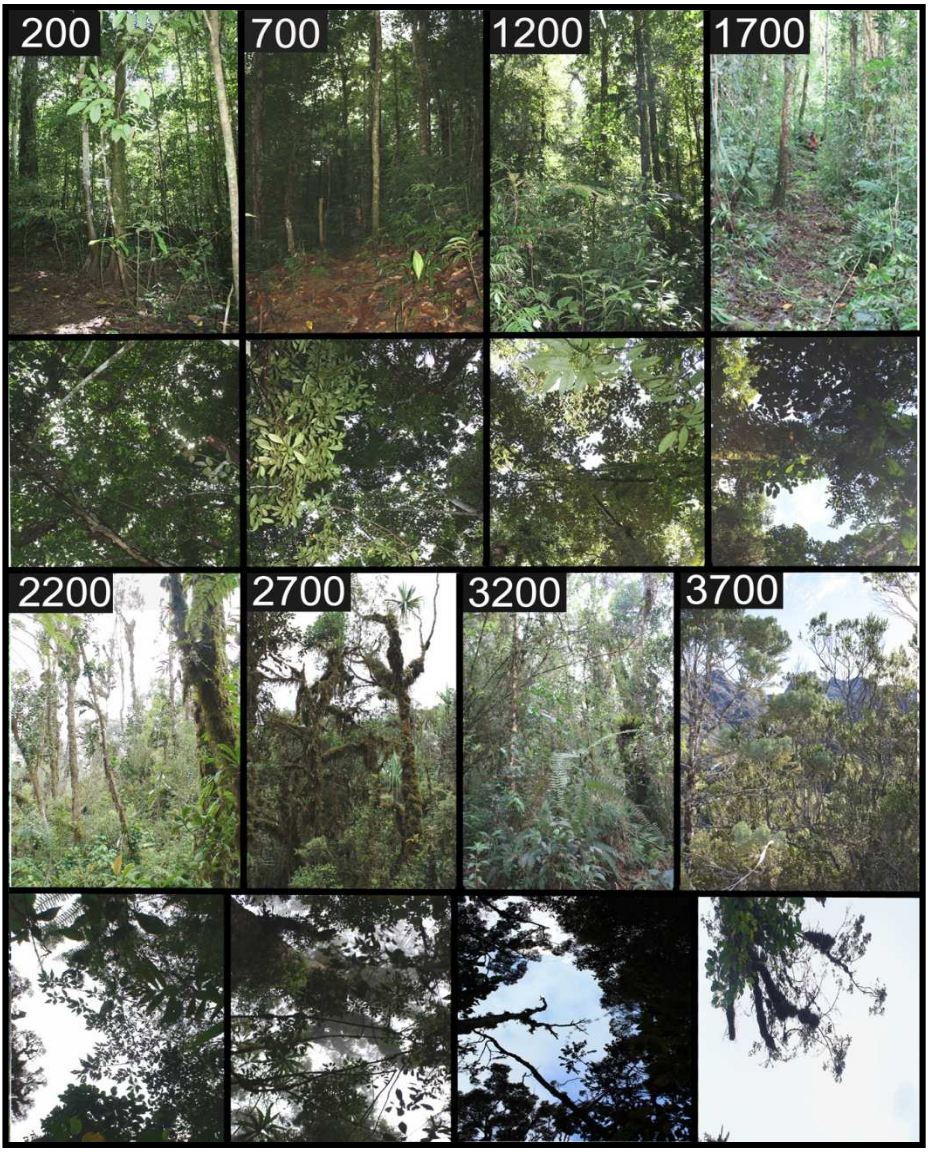
Table S4. Akaike's second-order information criterion (AICc) of the regression models of species richness of frugivorous birds across eight sites along altitudinal gradient, and their combinations. Models sorted according to ΔAICc.

Frugivores (82 species)	Log-likelihood	R^2	Akaike weight (w_1)	AIC_c	ΔAIC_c
Climate	1.00	0.98	0.23	52.69	0.00
Species pool	0.87	0.73	0.20	52.96	0.27
MDE * Species pool * Area	0.74	0.95	0.17	53.3	0.61
Species pool * Area	0.55	0.91	0.12	53.9	1.21
Area	0.52	0.81	0.12	54.01	1.32
Habitat	0.43	0.89	0.10	54.4	1.71
MDE * Area	0.27	0.83	0.06	55.32	2.63
Climate * Habitat * Species pool * Area	0.01	0.98	0.00	62.01	9.32
Climate * MDE * Habitat	0.01	0.98	0.00	62.03	9.34
Climate * Species pool * MDE * Area	0.01	0.98	0.00	62.03	9.34
MDE * Species pool	0.01	0.96	0.00	62.41	9.72
Habitat * Species * Climate * MDE * Area	0.01	0.95	0.00	62.6	9.91
Habitat * Area	0.01	0.92	0.00	63	10.31
Habitat * Species pool * MDE * Area	0.00	0.91	0.00	63.36	10.67
MDE	0.00	0.06	0.00	65.46	12.77
Climate * Area * MDE	0.00	0.99	0.00	80.57	27.88
Climate * Area	0.00	0.99	0.00	80.59	27.90
Climate * Species pool	0.00	0.98	0.00	80.68	27.99
Climate * Species pool * MDE	0.00	0.98	0.00	80.69	28.00
Habitat * Species pool * MDE	0.00	0.98	0.00	80.86	28.17
Habitat * Species pool * Climate	0.00	0.96	0.00	81.1	28.41
Area * MDE * Habitat	0.00	0.95	0.00	81.21	28.52
Climate * Habitat * MDE * Area	0.00	0.99	0.00	136.52	83.83
Climate * Species pool * Area	0.00	0.99	0.00	136.52	83.83
Climate * MDE	0.00	0.99	0.00	136.53	83.84
Habitat * Species pool	0.00	0.99	0.00	136.56	83.87
Habitat * Species pool * Climate * MDE	0.00	0.99	0.00	136.63	83.94
Climate * Habitat	0.00	0.99	0.00	Inf	Inf
Climate * Habitat * Area	0.00	0.99	0.00	Inf	Inf
Habitat * MDE	0.00	1.00	0.00	Inf	Inf
Habitat * Species pool * Area	0.00	0.99	0.00	Inf	Inf

Table S5. Akaike's second-order information criterion (AICc) of the regression models of species richness of omnivorous bird across eight sites along altitudinal gradient, and their combinations. Models sorted according to ΔAICc.

Omnivores (27 species)	Log-likelihood	R^2	Akaike weight (w_1)	AIC_c	ΔAIC_c
Climate	1.00	0.92	0.18	48.44	0.00
Species pool	0.98	0.77	0.17	48.49	0.05
Habitat	0.87	0.92	0.15	48.72	0.28
MDE * Area	0.78	0.91	0.14	48.93	0.49
Area	0.77	0.76	0.14	48.97	0.53
Species pool * Area	0.59	0.88	0.11	49.48	1.04
MDE * Species pool * Area	0.57	0.88	0.10	49.56	1.12
MDE * Species pool	0.01	0.95	0.00	57.51	9.07
Climate * Species pool * MDE * Area	0.01	0.92	0.00	57.70	9.26
Climate * MDE * Habitat	0.01	0.92	0.00	57.72	9.28
Climate * Habitat * Species pool * Area	0.01	0.92	0.00	57.77	9.33
Habitat * Area	0.01	0.93	0.00	57.93	9.49
Habitat * Species * Climate * MDE * Area	0.01	0.92	0.00	58.05	9.61
Habitat * Species pool * MDE * Area	0.01	0.92	0.00	58.06	9.62
MDE	0.00	0.01	0.00	62.39	13.95
Climate * Area * MDE	0.00	0.97	0.00	75.69	27.25
Climate * Species pool	0.00	0.96	0.00	75.80	27.36
Climate * Area	0.00	0.94	0.00	76.07	27.63
Climate * Species pool * MDE	0.00	0.92	0.00	76.34	27.90
Habitat * Species pool * Climate	0.00	0.93	0.00	76.45	28.01
Area * MDE * Habitat	0.00	0.93	0.00	76.60	28.16
Habitat * Species pool * MDE	0.00	0.92	0.00	76.71	28.27
Climate * MDE	0.00	0.98	0.00	131.47	83.03
Climate * Species pool * Area	0.00	0.98	0.00	131.48	83.04
Habitat * Species pool * Climate * MDE	0.00	0.98	0.00	131.51	83.07
Habitat * Species pool	0.00	0.97	0.00	131.59	83.15
Climate * Habitat * MDE * Area	0.00	0.97	0.00	131.60	83.16
Climate * Habitat	0.00	1.00	0.00	Inf	Inf
Climate * Habitat * Area	0.00	0.99	0.00	Inf	Inf
Habitat * MDE	0.00	1.00	0.00	Inf	Inf
Habitat * Species pool * Area	0.00	1.00	0.00	Inf	Inf

Figure S2. Forest interior and canopy openness at altitudinal sites. Each picture represents habitat with mean score for given altitude: 200 m – shrub density 8%, canopy openness 11%; 700 m – shrub density 12%, canopy openness 15%; 1200 m - shrub density 39%, canopy openness 16%; 1700 m - shrub density 40% (note the track); canopy openness 17%, 2200 m - shrub density 38%; canopy openness 40%; 2700 m - shrub density 34%, canopy openness 40%; 3200 m - shrub density 38%, canopy openness 21%; 3700 m - shrub density 20%, canopy openness 90%. Pictures are only illustrative as the measurements for each variable were averaged for each point.



Chapter II

New avian records and range shifts of birds along altitudinal gradient of Mt.Wilhelm, Papua New Guinea

Katerina Tvardikova
(manuscript in review)

Chapter II

New avian records and range shifts of birds along altitudinal gradient of Mt. Wilhelm, Papua New Guinea

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SUMMARY - East slopes of Mt. Wilhelm, the highest peak of Papua New Guinea, provide continuous rainforest altitudinal gradient ranging from 200 m to the tree line at 3,700 m. Based on the field work conducted in 2010 – 2012 and three expeditions along the Mt. Wilhelm altitudinal gradient; we present novel distributional information for 52 bird species. This includes range extensions, demographic data and altitudinal range shifts. We recorded 29 bird species with upwards range shifts compared to previously published literature, and tentatively conclude that upward (but not downward) range extensions and shifts are probably real, rather than resulting from poor quality of previous information. Complete list of species recorded during our work at eight altitudinal study sites includes 259 species.

The island of New Guinea has a complex geologic and tectonic history (Hall 2002) that has accounted for its complicated biogeography. Although birds are globally well known taxonomically, field research on New Guinea continues to uncover taxa new to science and complex biogeographical patterns (Diamond 1985; Beehler et al. 2007; Beehler and Prawiradilaga 2010). The island is divided into southern and northern watersheds by the comparatively well-explored Central Range (Diamond 1985). However, most of the Central Range was visited by Western ornithologists much later than smaller ranges, for example Fakfak region (1986 – by Doherty and Schadler from Rotschild and Leided Museums; Rheindt 2012) or Adalbert Mountains (Beehler et al. 1986). Despite its relatively good exploration, and improved access to the Central Range, ornithological exploration has been slow in the last decades. Recent expeditions were notable exceptions, and resulted in many discoveries, including up to four bird taxa new to science (Beehler et al. 2007; Beehler and Prawiradilaga 2010).

To our knowledge, there has been no intensive ornithological survey on the eastern slopes of Mt. Wilhelm. Usually, only the upper most altitudes are visited by keen bird-watchers, while lower valleys from Kegesugl to Bundi station and Brahmin station are poorly surveyed thanks to harsh track conditions. In 2010 – 2012, we conducted ornithological survey in the area with the goal to intensively survey avifauna across the altitudinal gradient, describe local avian diversity and record possible range extensions and range shifts or extensions.

METHODS

The study was performed on the eastern slopes of Mt. Wilhelm (4509 m a.s.l.) in the Central Range of Papua New Guinea. The complete rainforest gradient spanned from the lowland floodplains of the Ramu river (200 m a.s.l., S5° 44’ E145° 20’) to the timberline (3,700 m a.s.l., S5° 47’ E145° 03’; Fig. 1). The study was completed at eight sites within a distance of 60 km, and evenly spaced at 500 m altitudinal increment. Bird communities were surveyed by three standardized survey methods at each altitudinal site – by point counts, mist-netting and random walks through the area of. Point counts were carried out at 16 points regularly spaced along a 2,250 m transect and all birds seen or heard within radial distance 0 - 50 m were recorded. We completed 1792 point counts representing 448 hours counts during entirety of this study. Further, we mist-netted birds into 200 m long line of nets (using nets 2.5 m high x 12-18 m long, mesh 16 mm) from 5:30 am to 5:30 pm daily for 11 days at each site. Finally, we randomly walked (2 km^{-h}) across the surrounding area (~80 ha), and recorded all individual birds seen or heard. Random walking survey started at 3 pm and lasted till 5 or 6 pm. Here we report the overall list of species recorded during those standardized methods, as well as during the whole duration of expeditions. Photographs, recordings and observation data acquired during the studies are provided online to various global databases (i.e. GBIF) via New Guinea Birds encyclopedia (pngbirds.myspecies.info). Recording equipment Marantz PMD 620 & Microphone Seinnheiser ME67 was used for vocalization records and Canon 450 for photos. We adopted the species-level taxonomy of Handbook of the birds of the world (Hoyo et al. 1992-2011).

The first survey (9th April to 31th May 2010) included three replications of point counts, three mist-netting days and three random walks per altitude. The second survey (26th July and 15th October 2010) included replications of point counts, three mist-netting days and six random walks per altitude. The third survey (15th May 15th till July and 1st of August till 15th October 2012) including five point counts, three mist-netting days. In total, our data set for each site included 14 replications of point count surveys, 11 mist-netting days and 20 hours of random walks.

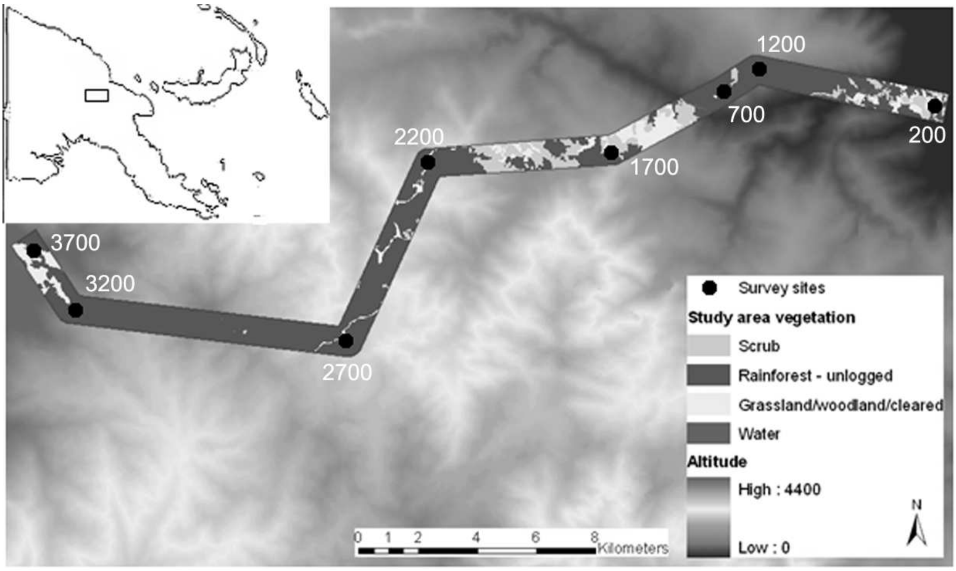

Figure 1. Location of altitudinal gradient of Mt. Wilhelm in Papua New Guinea (inserted map), and eight study sites along altitudinal gradient. Map courtesy of P.Shaerman & J.Bryan, UPNG Remote Sensing Centre, Papua New Guinea.

RESULTS

We recorded more than 34,000 bird individuals of 260 species across altitudinal sites on the slope of Mt. Wilhelm. While 208 of them were recorded within previously described altitudinal ranges and were expected in the region, 52 species had shifted or extended altitudinal range or were reported for the first time in the region (7 species). Noteworthy observations of the expeditions are summarized below and list of the species with recorded altitudinal ranges is provided.

Noteworthy and new observations

NEW GUINEA MEGAPODE *Megapodius decollatus*

The species known also as *Megapodius affinis* (but name *affinis* may not be applicable to present species, in which case *M. decollatus* would have priority) was previously recorded to be common from sea-level up to 2,100 m (Beehler et al. 1986), and even at 2,950 m (Freeman et al. 2013) in Huon Peninsula. We did not record the species higher than 700 m on the slopes of Mt. Wilhelm, and found the species to be very abundant at altitudes 200 – 700 m.

SALVADORI'S TEAL *Salvadorina waigiuensis*

Endemic to mountains of New Guinea, rare and local at lower altitudes but occurs across the island in suitable montane habitat. Previously unknown above 4,100 m

(Coates and Peckover 2001), we report observations at 4,500 m. Two individuals active early morning were observed in 2010.

GREAT-BILLED HERON *Ardea sumatrana*

Beehler et al. (1986) considered this a scarce resident throughout New Guinea's lowlands. Previously unknown from the region, we report the species at c. 300 m, on the river banks close to Brahmin station.

FOREST BITTERN *Zonerodius heliosylus*

Reported to occur at 100 - 300 m above sea level, but occasionally recorded up to 1430 m (Beehler et al. 1986). Here report the species at c. 1,650 m, close by Bundi Station, from the region without previous records.

BLACK-WINGED KITE *Elanus caeruleus*

The hunting attempt above shrubby area in the valley between 3,200 and 3,700 m were observed in 2011. Such observation is higher than expected altitudinal ranges (Beehler et al. 1986), and even higher than current report on upper limit of distribution from Mt. Hagen (GBIF records). The species seems to be rare in the surveyed region.

BRAHMINY KITE *Haliastur indus*

Previously unknown above 1,700 m (Coates and Peckover 2001), here we report species to be regular visitor at 2,200 m.

BLACK-MANTLED GOSHAWK *Accipiter melanochlamys*

Previously unknown above 3,000 m (Coates and Peckover 2001), and reported up to 2420 in Huon Peninsula (Freeman et al. 2013) we report the species regularly from c. 3500 m, overflying the valley to 3,200 m, both in 2010 and 2012.

MEYER'S GOSHAWK *Accipiter meyerianus*

Previously assumed to occur from sear sea-level to at least to 2,700 m (Beehler et al. 1986), we did not find the species above 2,200 m. However the species was recently observed in Mt. Hagen region, our records may be the first from the area on the eastern slopes of Mt. Wilhelm.

LITTLE EAGLE *Hieraaetus morphnoides*

On 26th September 2012, we made the one record of the species in this region. The species expected to occur all around New Guinea seems to be rare resident in the region, with more observation reported from south and west side of the Central Range, and the closest previous observation from Mt. Hagen.

FORBES'S FOREST RAIL *Rallina forbesi*
Bird was previously known from range 1,000 – 3,000 m (Coates and Peckover 2001), we reported to be quite common at altitudes between 2,200 – 3,200 m, and the most abundant at 2,700 m where we also mist-netted two individuals.

BARE-EYED RAIL *Gymnocrex plumbeiventris*
First observation of the bird in the region, recorded outside of the survey areas at 1,300 m, 20th September 2012. Previously reported altitudinal range is from sea-level to 1,200 m (Beehler et al. 1986), but with maximum up to 1,600 m in east New Guinea.

NEW GUINEA WOODCOCK *Scolopax saturate*
Known to occur in New Guinea mountains between 1,500 and 3,000 m (Beehler et al. 1986), here we report an observation from 2,700 m from region without previous records, but where the species was expected to occur (Beehler et al. 1986).

WHITE-THROATED PIGEON *Columba vitiensis*
Here we describe extension of altitudinal range, and report the species to be regularly seen at 2,700 m in 2010, and rarely in 2012. Commonly seen also at 2,200 m. Peckover and Filewood (1976) reported a mist-netted individual at 2,700 m, while Mayr (1941) considered the pigeon to be a lowland species with distribution up to 1,400 m.

BROWN CUCKOO-DOVE *Macropygia amboinensis*
In Papua New Guinea known to occur in mainland from sea level up to 1800, locally to 2100 m (Beehler et al. 1986). We report the species to be very common at all altitudes from 200 to 2,200 m, having similar abundances at all surveyed sites, while only slightly more abundant at 200 m.

BLACK-BILLED CUCKOO-DOVE *Macropygia nigrirostris*
The species is well known from the region, expected to occur from sea-level up to 2,600 m (Beehler et al. 1986), but we report the species only at 2,700 m. *Macropygia amboinensis,* a bird with similar vocalization is more common in the region, calling slowly, with more pronounced “whu” sylabes, while *Macropygia nigrirostris* has a rapidly descending higher pitched series of muted “kwok” notes decreasing in volume.

THICK-BILLED GROUND PIGEON *Trugon terrestris*

Known to inhabit rain forest and monsoon forest and lowlands and hills up to 640 m (Coates and Peckover 2001), but previously unknown from the region. Villagers killed one specimen at c. 1,100 m, but seen at sites 700 m.

PHEASANT PIGEON *Otidiphaps nobilis*

The previous highest-elevation record was 1,900 m (Beehler et al. 1986), and sound heard 2,050 m in Huon Peninsula (Freeman et al. 2013). We have seen 1 individual at 1,700 m in 2010 and three individuals at 2,200 m in 2010 and 2012. The species seems to be scarce throughout the region, similarly to situation in other ranges (Diamond 1985).

CORONETED FRUIT DOVE *Ptilinopus coronulatus*

While previously known up to 1,200 m (Beehler et al. 1986), we recorded the species at all altitudinal sites from 200 – 1,700 m. The observed individuals were identified as subspecies *quadrigeminus.*

ORNATE FRUIT DOVE *Ptilinopus ornatus*

Previously found primarily within altitude range of 200-1,350 m, but suspected to be apparently nomadic up to 2,500 m (Beehler et al. 1986). We confirm eight individuals from 2,200 m in 2010.

SHINING IMPERIAL PIGEON *Ducula chalconota*

Primary montane forest, generally at altitude range of 1,400 – 2,500 m, though occasionally down to 1100 m (Beehler et al. 1986). We have seen the species regularly between 1,700 – 2,700 m.

PESQUET'S PARROT *Psittrichas fulgidus*

The species is threatened by hunting, with a handful of records up to 2000 m (Beehler et al. 1986), and altitudinal range from 600 to 2,420 along Huon Peninsula (Freeman et al. 2013). We observed only two individuals at 2,200 m, confirming thus higher altitudinal range.

DUSKY LORY *Pseudeos fuscata*

With records up to 2,400 m (Beehler et al. 1986), we report altitudinal range extension, and species being very common at altitudes 2,200 m and 2,700 m, but present at 200, and from 1,700 to 2,700 m.

GOLDIE'S LORIKEET *Psitteuteles goldiei* (2,700 – 3,200 m)
Previously reported range up to 2,800 m (Beehler et al. 1986), and uncommon observations at 1,330 m and 1,600 m from Huon Peninsula (Freeman et al. 2013). We species to be common at 2,700 m and observed flock of seven individuals in two successive days at 3,200 m on a flowering tree together with *Astrapia stephaniae*.

PYGMY LORIKEET *Charmosyna wilhelminae* (700 – 1,200 m)
Uncommon and possibly overlooked species (Beehler et al. 1986) of mountain forest frequently descending into lowland forest at bases of mountains or at sea level, found from 1,000 to 2,200 m. We reported most of the individuals at 1,200 m but also some descending to 700 m.

RED-FRONTED LORIKEET *Charmosyna rubronotata* (200 m)
However previously reported only from north-western extremity of New Guinea, we observed individuals of genus *Charmosyna* with distinct red forecrown, and blue ear coverts (not blue coverts and red lores, cheeks and upper throat). The species was never observed together in flocks with *Charmosyna placensis* but once in mixed flock with *Lorius lory*.

BREHM'S TIGER PARROT *Psittacella brehmii* (2,200 – 2,700 m)
Previously reported to be resident from 1,500 to 2,600 in Central Range (Beehler et al. 1986), and inhabiting higher altitudinal range in Huon Peninsula from 1,700 m to at least 3,050 m, and being abundant at 2,700 – 3,050 m (Freeman et al. 2013). We report species present 2,200 – 2,700 m in Central Range, with two individuals mist-netted at 2,700 m.

CHESTNUT-BREASTED CUCKOO *Cacomantis castaneiventris*
A resident of hill forest at 500 – 2,300 m (Beehler et al. 1986), reported to range as low as 300 m in Huon Peninsula (Freeman et al. 2013). We mist-netted one individual at 200 m, and species was very common at altitudes 1,700 – 2,200 m, with only 3 individuals recorded at 2,700 m.

RUFOUS-THROATED BRONZE CUCKOO *Chrysococcyx ruficollis*
Previously was the species expected in montane forest and forest edges in highlands; mainly at 1,800 – 2,600 m, vagrant individuals up to 3,350 m (Beehler et al. 1986), and newly was reported from Huon Peninsula from 2,100, 2850 and 3,000 m (Freeman et al. 2013). We observed the species uncommonly at sites 2,700 and 3,200 m.

RUFOUS OWL *Ninox rufa*

This lowland species was known to occur only below 2,000 m (Marks et al. 1999). We observed few individuals active till 6 am, and associated the species with low-pitched double hoot, soft “hu-hu” at 1,700 m, which is possibly duet call of a pair.

BARKING OWL *Ninox connivens*

Their dog-like barking common at altitudes around Bundi village c. 1,500 m. Species is believed to predict a death in the village, in the direction from where the bird call. Altitudinal distribution of species in New Guinea is not known, but our observation higher than all other available records. All available records from New Guinea are scatter across eastern Highlands, Sepik, Karkar and Manam.

JUNGLE HAWK-OWL *Ninox theomacha*

Species known to occur up to c. 2,500 m, reported at 2,000 – 2,100 m by Frank Lambert, and at 30 m by Nick Anthas (Xeno-canto 2013). We report the species to be common from 200 - 2,200 m.

MARBLED FROGMOUTH *Podargus ocellatus*

Species expected to be mainly in lowlands, but recorded up to 800 m in Australia and to 1,500 m in New Guinea (Coates and Peckover 2001). We recorded the species at 1,200 – 2,200 m, and mist-netted at 1,700 m.

PACIFIC SWIFT *Apus pacificus*

Pacific swift is Asian species wintering in New Guinea and Australia. Similarly to previous records from Huon Peninsula (Freeman et al. 2013), we recorded this winter migrant till early June 2010 at 200 m, but only till April 2012 at the same sites. This would suggest that some populations stay in New Guinea instead of returning to Asia for breeding. Beehler et al. (1986) previously reported the bird only in southern watersheds and western Vogelkop.

MOUNTAIN KINGFISHER *Syma megarhyncha*

Previously reported from range 1,200 – 2,200 m (Beehler et al. 1986), we heard the species at 2,700 m and saw one individual along the track at c. 2,600 m. In most of the New Guinean mountains, *S. megarhyncha* replaces *S.torotoro* at altitude 1,000 m (Beehler et al. 1986). Despite our effort, we failed to record *S. torotoro* higher than 200 m, while our observations of *S. megarhyncha* would lead us to conclusion that the species was possibly overlooked. Given the difficulties with identification and observation of kingfishers in the field, further research would be needed to reveal possible presence of *S. torotoro* in the region, and altitudinal ranges of two species.

RAINBOW BEE-EATER *Merops ornatus*

Species is widespread in east Guinea and Australia, with main wintering ground for Australian birds in New Guinea, with some populations obviously resident all year round. We thus support those assumptions by observation of the species at 200 m during all surveys, throughout all years. *Merops philippinus* was not confirmed from the sites and all observed individuals had yellow-orange foreheads (not greenish), and broad black eye stripe, bordered with narrow blue line above (not white).

PAPUAN HORNBILL *Rhyticeros plicatus*

The species was recorded regularly from 200 to 1,200 m during censuses. One pair seen overfly Bundi station, and confirmed by villagers that species regularly come to their gardens at c. 1,500 – 1,600 m.

PAPUAN TREECREEPER *Cormobates placens*

The subspecies *steini* is known from west and central New Guinea from Weyland Mts. east through Hindenburg Range to Tari Gap area. The subspecies *meridionalis* is known from mountains of south-east New Guinea (east from Aseki area, Mt. Kaindi and Herzog Mts.). Two more recent records come from Tari Valley (Nick Anthas, Xeno-canto 2013). The species is known to occur between 1,250 – 2,600 m. We recorder the species at 2,630 m, outside of it's know range, but we were not able identify subspecies.

OBSCURE HONEYEATER *Lichenostomus obscurus*

We may report first record of the species for the region from 1,200 m. The subspecies *obscurus* was previously known to be patchily distributed on lower slopes of N, C & SE New Guinea east from Weyland Mts. (Hoyo et al. 1992-2011), from altitudes between 200 m and 1,100 m, occasionally as high as 1,400 m (Coates and Peckover 2001).

HILL-FOREST HONEYEATER *Meliphaga orientalis*

Mostly lower and middle mountains, from 550 m to c. 2,100 m, and only member of genus common (or present) above 1,400 (Beehler et al. 1986). We mist-netted the birds quite commonly at altitudinal sites from 1,700 to 2,700 m (seven individuals).

LONG-BEARDED HONEYEATER *Melidectes princeps*

The species endemic to few valleys on Mt. Giluwe, Mt. Hagen, and Kubor Range, known mainly from 3,000 – 3,800 m, but recently recorded to 4,200 m and extends as low as 2,750 m (Coates and Peckover 2001). On Mt. Wilhelm, reported to occur mainly above 3,050 m (Coates and Peckover 2001). We observed the species to be very abundant between 3,200 and 3,700 m at Mt.Wilhelm. Despite the effort, no individuals were reported in denser forest growths, and species seems to follow scattered trees along the tree line. While range restricted species endemic to small areas (the population at Mt. Wilhelm covers c. 200 ha) the species is one of the most common bird species recorded in the region. Specific relationship between locally endemic mites observed on local flowering *Rhododendrons* were observed, and needs to be further investigated.

CINNAMON-BREASTED HONEYEATER *Melidectes torquatus*

The species inhabits lower and middle montane forest, forest edges. Typically prefers semi-open habitats from 950 m to 1,900 m, and 1,200-1,700 in Central Range (Hoyo et al. 1992-2011). Along the gradient, we observed species to be common at sites 1,200 and 1,700 m, but indentified seven individuals also at 2,200 m. This can be due to very suitable conditions and many open areas along the tracks from Bundi station (1,700 m) to Sinopass (2,200 m), where many flowering trees were present along the road and adjacent gardens.

OLIVE-STREAKED HONEYEATER *Ptiloprora meekiana*

A resident of Saruwaged Mt.s (Huon Peninsula), Herzog Mts. and mountains of upper Mambare range and Mt. Tafa-Efogi. We bring the first record for its (subspecies *meekiana*) presence at c.2500 m. The birds were seen on along the track in May 2012, foraging on flowering tree. Call is non-distinctive “chip” or “schip“.

BICOLOURED MOUSE WARBLER *Crateroscelis nigrorufa*

The species is patchily distributed throughout foothill forest of New Guinea, with very restricted altitudinal range (Beehler et al. 1986). We found the species to e abundant at 1,700 m, and even more individuals singing uphill around 1,770 – 1,790 m. The surprising local abundance of this species with restricted range, in comparison, there are just 38 specimen records in ORNIS database from anywhere around Papua New Guinea (Freeman et al. 2013).

BUFF-FACED SCRUBWREN *Sericornis perspicillatus* (1,700 – 2,700 m)/ **PAPUAN SCRUBWREN** *Sericornis papuensis* (1,700 – 3,200 m)

Two similar species (S. *perspicillatus* and *papuensis),* differ strongly in its vocalization and could be easily distinguished in the forest while singing. In hand, Papuan Scrubwren posses dark subterminal tail-band (95%, N = 64), and brownish-buff crown and forecrown. Buff-faced Scrubwren has crown grey and subterminal tail-band was not observed in individuals inspected by K.Tvardikova (~70%, N = 73). Along the gradient, S. *perspicillatus* was very abundant at altitudes 1,700 – 2,200 m with abundances decreasing towards 2,700, while S. *papuensis* was getting more abundant towards upper range limits at 3,200 m.

STOUT-BILLED CUCKOO-SHRIKE *Coracina caeruleogrisea*

In New Guinea was known mainly in lowlands, hill forest and lower mountains, present from sea-level up to 1,700 m, rarely up to 2,450 m (Beehler et al. 1986). Species was recorded also at Tari gap at 2500 m in 1990 by Niels Poul Dreyer (Xeno-canto 2013). We observed individuals feeding at 2,700 m in September 2012, and heard the distinctive sound often at all sites between 700 to 2,700 m, and mist-netted male at 2,200 m.

GOLDEN CUCKOO-SHRIKE *Campochaera sloetii*

The species was previously known only from Arfak Mts. and east to Wawak area (subspecies *sloetii*) and from south New Guinea lowlands from Range Mimika east to Moroka, and foothills of Owen Stanley Range (subspecies *flaviceps*) (Hoyo et al. 1992-2011), but we made observations at altitudinal sites 200 and 1,200 m. Also our other surveys across Madang lowlands confirmed the species to be rare resident patchily distributed along Ramu river.

BLACK SICKLEBILL *Epimachus fastuosus* (1,200 – 2,700 m)/**BROWN SICKLEBILL** *Epimachus meyeri* (1,700 – 3,200 m)

Sicklebills are known from middle montane primary forest, more rarely in adjacent second growth and garden edges. *E. fastuosus* were previously described from 1,280 – 2,550 m, mainly in narrow elevational zone of 1,800 - 1,500 m; and predominate at lower elevation than *E. meyeri*. We observed the ranges to be broadly overlapped, with *E. meyeri* very abundant and *E. fastuosus* observed only in few individuals.

RUFOUS-COLLARED MONARCH *Arses insularis*

Previously known to have altitudinal range from 230 – 1,200 m (Beehler et al. 1986; Freeman et al. 2013), we observed and mist-netted the species often at sites from 200 to 1,700 m.

BLACK SITTELLA *Daphoenositta miranda*

We present first records for the species, which was previously, known for the same altitudes from Snow Mts, Kubor Range, Mt. Giluwe, Mt. Tafa, Mt. Scratchley and Mt. Albert Edward (Hoyo et al. 1992-2011). The species is rare resident between 2,700 and 3,700 m of the gradient.

TREEFERN GERYGONE *Gerygone ruficollis*

This montane species was previously recorded from 1100 upwards, to c. 3300 m in Snow Mts. and south-east New Guinea; being the most common at lower and middle altitudes. Recently found to be abundant at 1300 m in Fakfak mountains (Rheindt 2012). Despite the effort, we failed to confirm the presence lower than 1,700 m, but reported range extensions up to tree line at 3,700 m.

VARIABLE PITOHUI *Pitohui kirhocephalus* (200 – 1,200 m)/**HOODED PITOHUI** *Pitohui dichrous* (700 – 1,700 m)

Those sister species (Dumbacher et al. 2008) appear to replace each other altitudinally over most of the New Guinea ranges (Beehler et al. 1986). We confirm *P. kirhocephalus* to be lowland species, while *P.dichorus* inhabits higher altitudes. On the other hand, we can't confirm strictly exclusive ranges. At site 1,200 m, both species were seen in syntopy (recorded to have exactly the same abundances), and sometimes recorded at the same point. The abundance patters do not suggest that species are widely sympatric; rather our locality may lie at an altitude where species are in narrow contact. The zone of transition is however much higher than previously reported in Fakfak Mts. (Rheindt 2012).

The list of 208 recorded species with observed altitudinal distribution:

DWARF CASSOWARY Casuarius bennetti (2,700 m)
WATTLED BRUSH TURKEY *Aepypodius arfakianus* (1,700 m)
BROWN-COLLARED BRUSH TURKEY *Talegalla jobiensis* (1,200 m)
PACIFIC BLACK DUCK *Anas superciliosa* (3500 m)
LONG-TAILED BUZZARD *Henicopernis longicauda* (200 – 700 m)
BLACK KITE *Milvus migrans* (200 – 1700 m)
WHISTLING KITE *Haliastur sphenurus* (200 – 700 m)
GREY GOSHAWK *Accipiter novaehollandiae* (700 m)
PAPUAN HARPY EAGLE *Harpyopsis novaeguineae* (200 – 1200 m, 2200 – 3200 m)
GREAT CUCKOO-DOVE *Reinwardtoena reinwardtii* (200 - 3,200 m)

EMERALD DOVE *Chalcophaps indica (200 - 700 m)*
STEPHAN'S DOVE *Chalcophaps stephani* (200 – 1,200 m)
NEW GUINEA BRONZEWING *Henicophaps albifrons* (200 – 1,200 m)
WHITE-BIBBED GROUND DOVE *Gallicolumba jobiensis* (2,200 m)
BRONZE GROUND DOVE *Gallicolumba beccarii* (1,200 – 1,700 m)
WOMPOO FRUIT DOVE *Ptilinopus magnificus* (700 – 1,200 m)
PINK-SPOTTED FRUIT DOVE *Ptilinopus perlatus* (200 – 700 m)
SUPERB FRUIT DOVE *Ptilinopus superbus* (200 – 2,200 m)
BEAUTIFUL FRUIT DOVE *Ptilinopus pulchellus* (200 – 1,200 m)
WHITE-BIBBED FRUIT DOVE *Ptilinopus rivoli* (1,700 – 3,200 m)
ORANGE-BELLIED FRUIT DOVE *Ptilinopus iozonus* (200 m)
PURPLE-TAILED IMPERIAL PIGEON *Ducula rufigaster* (200 m)
PINON'S IMPERIAL PIGEON *Ducula pinon* (200 m)
ZOE'S IMPERIAL PIGEON *Ducula zoeae* (200 – 1,200 m)
PAPUAN MOUNTAIN PIGEON *Gymnophaps albertisii* (1,700 – 3,700 m)
ORANGE-FRONTED HANGING PARROT *Loriculus aurantiifrons* (200 m)
BUFF-FACED PYGMY PARROT *Micropsitta pusio* (200 – 700 m)
RED-BREASTED PYGMY PARROT *Micropsitta bruijnii* (700 – 1,200 m)
PALM COCKATOO *Probosciger aterrimus* (200 – 1,200 m)
SULPHUR-CRESTED COCKATOO *Cacatua galerita* (200 – 1,200 m)
RAINBOW LORIKEET *Trichoglossus haematodus* (200 – 1,200 m)
BLACK-CAPPED LORY *Lorius lory* (200 – 1,200 m)
RED-FLANKED LORIKEET *Charmosyna placentis* (200 – 700 m)
PAPUAN LORIKEET *Charmosyna papou* (1,700 – 3,700 m)
PLUM-FACED LORIKEET *Oreopsittacus arfaki* (1,700 – 3,700 m)
YELLOW-BILLED LORIKEET *Neopsittacus musschenbroekii* (1,200 – 3,200 m)
ORANGE-BILLED LORIKEET *Neopsittacus pullicauda* (1,700 – 3,700 m)
PAINTED TIGER PARROT *Psittacella picta* (2,700 – 3,700 m)
RED-CHEEKED PARROT *Geoffroyus geoffroyi* (200 m)
BLUE-COLLARED PARROT *Geoffroyus simplex* (700 m)
ECLECTUS PARROT *Eclectus roratus* (200 – 1,200 m)
PAPUAN KING PARROT *Alisterus chloropterus* (700 – 2,700 m)
ORANGE-BREASTED FIG PARROT *Cyclopsitta gulielmitertii* (200 m)
DOUBLE-EYED FIG PARROT *Cyclopsitta diophthalma* (200 – 1,700 m)
EDWARDS'S FIG PARROT *Psittaculirostris edwardsii* (200 – 1,200 m)
BRUSH CUCKOO *Cacomantis variolosus* (200 – 1,700 m)
FAN-TAILED CUCKOO *Cacomantis flabelliformis* (1,200 - 3,700 m)
LITTLE BRONZE CUCKOO *Chrysococcyx minutillus* (200 m)
WHITE-CROWNED KOEL *Caliechthrus leucolophus* (200 – 1,200 m)
DWARF KOEL *Microdynamis parva* (200 m)
COMMON KOEL *Eudynamys scolopaceus* (200 – 1,200 m)
CHANNEL-BILLED CUCKOO *Scythrops novaehollandiae* (200 m – winter migrant)
PHEASANT-COUCAL *Centropus phasianinus* (200 – 700 m)
LARGE-TAILED NIGHTJAR *Caprimulgus macrurus* (200 m)
FELINE OWLET-NIGHTJAR *Euaegotheles insignis* (2,700 m)
MOUNTAIN OWLET-NIGHTJAR *Aegotheles albertisi* (2,200 m)
GLOSSY SWIFTLET *Collocalia esculenta* (200, 1,500 – 2,700 m)
MOUNTAIN SWIFTLET *Aerodramus hirundinaceus* (3,700 m)
DOLLARBIRD *Eurystomus orientalis* (200 – 700 m)
HOOK-BILLED KINGFISHER *Melidora macrorrhina* (200 – 700 m)
COMMON PARADISE KINGFISHER *Tanysiptera galatea* (200 – 700 m)
SHOVEL-BILLED KOOKABURRA *Clytoceyx rex* (1,700 – 2,200 m)
RUFOUS-BELLIED KOOKABURRA *Dacelo gaudichaud* (200 – 700 m)
FOREST KINGFISHER *Todiramphus macleayii* (1,700 m)
YELLOW-BILLED KINGFISHER *Syma torotoro* (200 m)
VARIABLE DWARF KINGFISHER *Ceyx Lepidus* (200 – 1,200 m)
AZURE KINGFISHER *Alcedo azurea* (200 – 1,200 m)

Little Kingfisher *Alcedo pusilla* (200 m)
Red-bellied Pitta *Pitta erythrogaster* (200 – 700 m)
Hooded Pitta *Pitta sordida* (200 – 700 m)
White-eared Catbird *Ailuroedus buccoides* (200 – 1,700 m)
Black-eared Catbid *Ailuroedus melanotis* (2,200 m)
MacGregor's Bowerbird *Amblyornis macgregoriae* (2,200 – 3,200 m)
Yellow-breasted Bowerbird *Chlamydera lauterbachi* (2,200 m)
White-shouldered Fairy-wren *Malurus alboscapulatus* (1,700 – 2,200 m)
Orange-crowned Wren *Clytomyias insignis* (2,700 - 3,200 m)
Tawny-breasted Honeyeater *Xanthotis flaviventer* (700 – 1,200 m)
Black-throated Honeyeater *Lichenostomus subfrenatus* (1,700 – 3,700 m)
White-marked Forest Honeyeater *Meliphaga montana* (700 – 1,200 m)
Mimic Honeyeater *Meliphaga analoga* (200 – 1,700 m)
Puff-backed Honeyeater *Meliphaga aruensis* (200 – 1,200 m)
Plain Honeyeater *Pycnopygius ixoides* (200 – 1,200 m)
Meyer's Friarbird *Philemon meyeri* (200 – 1,200 m)
Helmeted Friarbird *Philemon buceroides* (200 – 700 m)
Smoky Honeyeater *Melipotes fumigatus* (1,200 – 3,700 m)
Sooty Honeyeater *Melidectes fuscus* (2,200 – 3,700 m)
Yellow-browed Honeyeater *Melidectes rufocrissalis* (1,700 m)
Belford's Honeyeater *Melidectes belfordi* (2,200 – 3,700 m)
Rufous-backed Honeyeater *Ptiloprora guisei* (1,700 – 3,200 m)
Black-backed Honeyeater *Ptiloprora perstriata* (2,200 – 3,700 m)
Long-billed Honeyeater *Melilestes megarhynchus* (200 – 2,200 m)
Red-collared Honeyeater *Myzomela rosenbergii* (1,200 – 3,700 m)
Olive Straight-bill *Timeliopsis fulvigula* (1,700 m)
Green-backed Honeyeater *Timeliopsis fallax* (700 m)
Lowland Mouse Warbler *Crateroscelis murina* (200 – 1,700 m)
Mountain Mouse Warbler *Crateroscelis robusta* (1,200 – 3,700 m)
Pale-billed Scrubwren *Sericornis spilodera* (700 – 1,200 m)
Grey-green Scrubwren *Sericornis arfakianus* (1,200 – 1,700 m)
Large Scrubwren *Sericornis nouhuysi* (1,700 – 3,700 m)
Yellow-bellied Gerygone *Gerygone chrysogaster* (200 – 700 m)
Grey Gerygone *Gerygone cinerea* (1,700 – 3,200 m)
Green-backed Gerygone *Gerygone chloronota* (200 - 1,200 m)
Fairy Gerygone *Gerygone palpebrosa* (200, 1,200 m)
Papuan Thornbill *Acanthiza murina* (2,700 – 3,700 m)
Isidore's Rufous Babbler *Garritornis isidorei* (200 m)
Loria's Cnemophilus *Cnemophilus loriae* (1,700 – 3,200 m)
Crested Cnemophilus *Cnemophilus macgregorii* (2,200 – 3,700 m)
Yellow-breasted Cnemophilus *Loboparadisea sericea* (1,700 m)
Black Berrypecker *Melanocharis nigra* (200 - 1,200 m)
Lemon-breasted Berrypecker *Melanocharis longicauda* (1,700 m)
Fan-tailed Berrypecker *Melanocharis versteri* (1,700 – 3,700 m)
Streaked Berrypecker *Melanocharis striativentris* (1,700, 2,700 m)
Plumed Longbill *Oedistoma iliolophus* (700 – 1,700 m)
Yellow-bellied Longbill *Toxorhamphus novaeguineae* (200 – 1,200 m)
Slaty-chinned Longbill *Toxorhamphus poliopterus* (1,200 – 2,200 m)
Tit-Berrypecker *Oreocharis arfaki* (2,200 – 3,700 m)
Crested Berrypecker *Paramythia montium* (2,700 – 3,700 m)
Spotted Jewel-babbler *Ptilorrhoa leucosticta* (1,700 – 2,700 m)
Blue Jewel-babbler *Ptilorrhoa caerulescens* (200 – 1,200 m)
Chestnut-backed Jewel-babbler *Ptilorrhoa castanonota* (1,200 m)
Yellow-breasted Boatbill *Machaerirhynchus flaviventer* (200 – 1,200 m)
Black-breasted Boatbill *Machaerirhynchus nigripectus* (1,700 – 3,200 m)
Black Butcherbird *Cracticus quoyi* (200 m)
Hooded Butcherbird *Cracticus cassicus* (200 – 700 m)

Lowland Peltops *Peltops blainvillii* (200 – 700 m)
Mountain Peltops *Peltops montanus* (1,700 – 2,700 m)
Great Woodswallow *Artamus maximus* (2,700 – 3,700 m)
Boyer's Cuckoo-shrike *Coracina boyeri* (200 – 1,200 m)
White-bellied Cuckoo-shrike *Coracina papuensis* (200 – 1,700 m)
Hooded Cuckoo-shrike *Coracina longicauda* (2,700 m)
Cicadabird *Coracina tenuirostris* (200 – 1,200 m)
Black-shouldered Cuckoo-shrike *Coracina incerta* (200 – 700 m)
New Guinea Cuckoo-shrike *Coracina melas* (200 m)
Black-bellied Cuckoo-shrike *Coracina montana* (1,200 – 2,700 m)
Black-browned Triller *Lalage atrovirens* (200 m)
Wattled Ploughbill *Eulacestoma nigropectus* (2,700 m)
Goldenface *Pachycare flavogriseum* (1,200 – 2,200 m)
Mottled Whistler *Rhagologus leucostigma* (1,700 – 2,700 m)
Rufous-naped Whistler *Aleadryas rufinucha* (1,700 – 3,700 m)
Rusty-breasted Whistler *Pachycephala hyperythra* (200 – 1,700 m)
Brown-backed Whistler *Pachycephala modesta* (2,700 – 3,200 m)
Grey Whistler *Pachycephala simplex* (700 – 1,200 m)
Sclater's Whistler *Pachycephala soror* (1,200 – 2,200 m)
Regent Whistler *Pachycephala schlegelii* (1,700 – 3,700 m)
Brown Oriole *Oriolus szalayi* (200 – 700 m)
Little Shrike-thrush *Colluricincla megarhyncha* (200 – 2,200 m)
Rusty Pitohui *Pitohui ferrugineus* (200 m)
Crested Pitohui *Pitohui cristatus* (1,200 m)
Black Pitohui *Pitohui nigrescens* (1,700 – 2,200 m)
Pygmy Drongo *Chaetorhynchus papuensis* (200 – 1,700 m)
Spangled Drongo *Dicrurus bracteatus* (200 – 700 m)
Northern Fantail *Rhipidura rufiventris* (200 – 1,700 m)
Sooty Thicket Fantail *Rhipidura threnothorax* (200 – 1,200 m)
White-bellied Thicket Fantail *Rhipidura leucothorax* (200 – 1,200 m)
Black Fantail *Rhipidura atra* (200 – 2,700 m)
Friendly Fantail *Rhipidura albolimbata* (1,700 – 3,700 m)
Dimorphic Fantail *Rhipidura brachyrhyncha* (1,200 – 3,700 m)
Rufous-backed Fantail *Rhipidura rufidorsa* (200 – 700 m)
Black Monarch *Monarcha axillaris* (1,200 – 2,700 m)
Rufous Monarch *Monarcha rubiensis* (200 m)
Black-winged Monarch *Monarcha frater* (200 – 1,200 m)
Spot-winged Monarch *Monarcha guttula* (200 – 1,200 m)
Hooded Monarch *Monarcha manadensis* (200 m)
Golden Monarch *Monarcha chrysomela* (200 – 1,200 m)
Shining Flycatcher *Myiagra alecto* (200 – 1,700 m)
Grey Crow *Corvus tristis* (200 – 1,700 m)
Lesser Melampitta *Melampitta lugubris* (2,700 – 3,700 m)
Blue-capped Ifrit *Ifrita kowaldi* (1,700 – 3,700 m)
Crinkle-collared Manucode *Manucodia chalybatus* (700 – 1,200 m)
Princess Stephanie's Astrapia *Astrapia stephaniae* (2,700 – 3,700 m)
Superb Bird-of-Paradise *Lophorina superba* (1,700 m)
Magnificent Riflebird *Ptiloris magnificus* (200 – 700 m)
Magnificent Bird-of-Paradise *Diphyllodes magnificus* (700 – 1,700 m)
King Bird-of-Paradise *Cicinnurus regius* (200 – 700 m)
Lesser Bird-of-Paradise *Paradisaea minor* (200 – 1,200 m)
Ashy Robin *Poecilodryas albispecularis* (1,200 – 1,700 m)
Black-sided Robin *Poecilodryas hypoleuca* (200 – 1,200 m)
Black-bibbed Robin *Poecilodryas albonotata* (2,200 – 3,200 m)
White-winged Robin *Peneothello sigillata* (2,700 – 3,700 m)
Blue-grey Robin *Peneothello cyanus* (1,700 – 2,700 m)
White-rumped Robin *Peneothello bimaculata* (700 – 1,700 m)

WHITE-FACED ROBIN *Tregellasia leucops* (200 – 1,700 m)
WHITE-EYED ROBIN *Pachycephalopsis poliosoma* (1,200 – 1,700 m)
MONTANE FLYCATCHER *Microeca papuana* (1,700 – 3,200 m)
TORRENT FLYCATCHER *Monachella muelleriana* (200 m)
YELLOW-LEGGED FLYCATCHER *Microeca griseoceps* (1,200 m)
OLIVE-YELLOW FLYCATCHER *Microeca flavovirescens* (200 – 1,200 m)
GARNET ROBIN *Eugerygone rubra* (1,700 – 3,700 m)
LESSER GROUND ROBIN *Amalocichla incerta* (1,700 m)
PACIFIC SWALLOW *Hirundo tahitica* (200 – 2,200 m)
ISLAND LEAF WARBLER *Phylloscopus poliocephalus* (1,200 – 2,200 m)
BLACK-FRONTED WHITE-EYE *Zosterops minor* (200 – 1,200 m)
NEW GUINEA WHITE-EYE *Zosterops novaeguineae* (1,700 – 2,700 m)
SHINING STARLING *Aplonis metallica* (200 – 700 m)
SINGING STARLING *Aplonis cantoroides* (200 m)
YELLOW-FACED Myna *Mino dumontii* (200 – 700 m)
ISLAND THRUSH *Turdus poliocephalus* (2,700 – 3,700 m)
PIED BUSHCHAT *Saxicola caprata* (2,200 m)
RED-CAPPED FLOWERPECKER *Dicaeum geelvinkianum* (200 – 2,200 m)
BLACK SUNBIRD *Leptocoma sericea* (200 – 1,200 m)
OLIVE-BACKED SUNBIRD *Cinnyris jugularis* (200 – 1,700 m)
STREAK-HEADED MANNIKIN *Lonchura tristissima* (200 m)
BLUE-FACED PARROTFINCH *Erythrura trichroa* (1,700 – 3,700 m)
HOODED MANNIKIN *Lonchura spectabilis* (2,200 m)
ALPINE PIPIT *Anthus gutturalis* (3,200 – 3,700 m)
MOUNTAIN FIRETAIL *Oreostruthus fuliginosus* (3,700 m)

DISCUSSION

Mountains of Central Range are considered to be among the more ornithologicaly explored regions (unlike outlying mountain ranges and some parts of lowlands (Rheindt 2012). Despite several months spend along altitudinal gradient of Mt. Wilhelm in years 2010 – 2011, our further survey in the area in 2012 resulted into addition of 11 species. Altogether, our work added at least seven new species to the avifauna of the region on the east slopes of Mt. Wilhelm. (at least *Daphoenositta miranda*, *Campochaera sloetii*, *Ptiloprora meekiana*, *Lichenostomus obscurus*, *Cormobates placens*, *Charmosina rubronata*, *Ardae sumatrana*, and possibly also *Zonerodius heliosylus*, *Accipiter meyerianus* and *Trugon terrestris*). Many of those species were previously observed only in other parts of Central Range, or lowlands in Sepik basin (Beehler et al. 1986; Coates and Peckover 2001). Despite our effort, we did not record some specie we regularly find in other regions along Ramu river and Madang lowlands. Those were Northern Cassowary *Cassuarius unappendiculatus*, Victoria Crowned Pigeon *Goura victoria*. We also reported populations of two migratory species (*Apus pacificus*, *Merops ornatus*) to be resident in the area all year round. More importantly, we observed numerous (minimum of 29 species which represent 11 % of bird species) shifts and extensions of altitudinal ranges. This discovery is especially surprising, taking into account the altitudinal distance of 500 m between study sites, resulting in significant underestimation of range limits at the altitudes in between, and by fact that we did not consider shifts up to 100 m altitudinal to be significant.

Shifts in geographic ranges are common in temperate regions, where species may respond to a climate warming by moving to higher latitudes or elevations. The few studies that refer to elevation range extensions for tropical birds (Pounds et al. 1999; Peh 2007) rely on indirect evidence, derived from community changes in census plots (Pounds et al. 1999) or changes in elevation limits inferred from bird lists (Peh 2007). Baseline information on the abundance of species along elevation gradients is however essential to determine whether species shift in elevation and, if so, by how much (Shoo et al. 2006). It is worth to mention that we observed mostly (29) upward shifts or extensions of ranges, while only two species were reported lower than expected (downward shift of *Charmosyna wilhelminae*, and range extension of *Cacomantis castaneiventris*) based on the previously published information. We are aware that previously reported ranges may include mistakes, may not be exact or may be specific to a particular geographic region. It is however unlikely that the historical information would systematically underestimate only upper altitudinal limits. In concordance with previous studies (Forero-Medina et al. 2011), we also found more altitudinal shifts in frugivorous birds (16 species) than in insectivores (7 species).

Other caveats may be that many frugivorous species are good altitudinal migrants and could seasonally follow the resources – flowering or fruiting trees (Loiselle and Blake 1990). On the other hand, the observed shifts seem to be repeated throughout three independent surveys during years, and we repeatedly observed some species at higher than expected altitudes. Although the results should be considered with caution, they do indicate a consistent pattern of upward direction of the range shifts.

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Chapter III

Diet of land birds along an altitudinal gradient in Papua New Guinea

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(manuscript in review)

Diet of land birds along altitudinal gradient in Papua New Guinea

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Abstract

We studied feeding specialization of birds in Papua New Guinea along a complete rainforest altitudinal gradient from 200 to 3700 m a.s.l. We classified bird species to feeding guilds by cluster analysis based on the composition of food samples regurgitated from mist-netted birds during a 12-month study. The proportion of insectivores decreased from 75% of all species, based on data from the literature, to 42% based on our data, as many presumably insectivorous species also fed partly on fruits or nectar. Diversity of food items taken decreased with altitude, and both the relative importance of arthropods and their size differed between habitats for individual bird species. The abundance of all invertebrates and Hymenoptera per food sample decreased with altitude; that of Hemiptera and Lepidoptera did not change with altitude, whilst the abundance of Coleoptera and Diptera followed a hump-shaped distribution with the maximum abundance being found at mid-altitudes. Coleoptera were the most exploited arthropods, followed by Araneae, Hymenoptera and Lepidoptera (caterpillars). This reflects both opportunism with respect to food items and the relative importance of individual arthropod groups for bird diet in this tropical forest. The mean body weight of the arthropods taken by birds decreased with the altitude and was positively correlated with mean body weight in bird communities. The mean body weight of birds also decreased with altitude. However, there was no

correlation between the mean weight of arthropod individuals in the diet and the weight of individual birds within bird species.

Key words: altitude, arthropod, bird diet, feeding guilds, opportunism, regurgitation, tartar emetic

INTRODUCTION

Diets of land birds are rarely directly examined by avian ecologists, and this is especially true for entire bird communities (Rosenberg and Cooper 1990a). Existing information is usually based on samples from a few individuals per species only (Hoyo et al. 1992-2011), detailed knowledge of bird diets is critical to our understanding of avian ecology and the importance of birds as predators, herbivores and seed dispersers. The diet of tropical species, including species in New Guinea, is particularly poorly known (Collins et al. 1990; Karr and Brawn 1990; Loiselle and Blake 1990). The feeding preference for most tropical bird species is usually inferred from a few individual observations, or is totally unknown. Quantitative data on their diet are nevertheless important for the understanding of food webs in bird communities (Poulin et al. 1994a).

A large proportion of existing diet data has been obtained destructively by dissecting stomachs of birds in museum collections (e.g. (Dumbacher et al. 2004), (Rosenberg and Cooper 1990b)). The analysis of fecal samples (Loiselle and Blake 1990), forced flushing (Moody 1970; Laursen 1978) and forced regurgitation are the most frequently used non-destructive methods for investigating the diets of passerines. Forced regurgitation has been performed with water (Ford et al. 1982; Majorr 1990) and several emetics (Prys-Jones et al. 1974; Radke and Frydendall 1974). Different methods for obtaining food samples are described and their advantages and limitations discussed by Rosenberg and Cooper (1990a). Most studies have used antimony potassium tartar, which has proved to be a successful emetic in many bird families (Prys-Jones et al. 1974; Robinson and Holmes 1982; Poulin et al. 1994a, b; Poulin et al. 1994c; Poulin and Lefebvre 1995; Sekercioglu et al. 2002). Poulin (1994c) proved the efficiency of antimony potassium tartrate (tartar emetic) on a large sample of tropical and migrant land birds.

Biologists have quantified bird diets in diverse ways. The key parameters include diet breadth (Yoshikawa and Isagi 2012), overlap (Sekercioglu et al. 2002; Auer and Martin 2012), and spatial (Robinson and Holmes 1982; Sekercioglu et al. 2002) and temporal (Burger et al. 2012) fluctuation. Observed diet has also been related to food availability (Raley and Anderson 1990). Several studies have identified body size of prey as an important factor of prey choice by birds (Janes 1994; Woodward et al. 2005; Brose et al. 2006; Philpott et al. 2009; Brose et al. 2012). In particular, body size of birds is positively correlated with body size of their prey (Bédard 1969; Cohen et al. 1993), including in insectivorous birds (Hespenheide 1971). Consequently the species composition and size distribution of prey may influence the distribution and survival of birds and therefore affect the structure of avian guilds in different habitats (Holmes et al. 1979; Janes 1994); but see (Sekercioglu 2012), (Champlin et al. 2009). The importance of prey choice and prey size distribution in different habitats by avian species has attracted relatively little attention.

To redress these gaps, we used emetic tartar to estimate the diet of birds across different forest habitats on a large geographic scale, including an altitudinal gradient, in Papua New Guinea. We analyzed four dietary parameters: prey type (used to estimate the diet similarity of bird species), diversity of prey types (to measure diet breadth), relative abundance of prey morphospecies within food samples (to assess prey dispersion), and prey size distribution (to correlate the size of predator and prey across different habitats). Based on these dietary parameters, we discuss four general questions: (1) What food is taken by individual species? (2) Are tropical birds diet opportunists or specialists? (3) Are there trends in opportunism and specialization along altitudinal gradient? (4) How does bird diet differ along a complete altitudinal gradient?

METHODS

The study was carried out at 10 study sites in Papua New Guinea. Eight study sites were regularly spaced, from 200 to 3700 m a.s.l. with 500 m altitudinal increments, along an altitudinal gradient at Mt. Wilhelm (-5. 44, 145.20; -5. 47, 145. 03). The other areas were located in the Saruwaged Mts. (Kotet: 1700m a.s.l., -5.87, 146.37) and in Madang district (Wanang 3: 159 m a.s.l., -5.22, 145.08). Data from Wanang were combined with site 200m a.s.l. at altitudinal gradient for some of the analyzes focused on altitudinal patterns. Similarly, data from Kotet were combined with the Mt. Wilhelm 1700 m a.s.l. data.

We mist-netted birds (under license CZ1062) at 10 sites throughout the years 2010 and 2011 using 200 meters (2.5 x 18 or 12 m, 16 mm mesh) of nets per site. At each study site we had mist-nets open for three days (from 05:30 to 17:30 Standard time, mist-nets visited in 20-min intervals) during wet season, and three days in dry season. Only the Kotet site was surveyed in two three-day periods, which were separated by only 20 days due to poor accessibility. At all sites, birds were captured, weighed, measured, identified to species and sex (where possible), banded with a colorful ring and forced to regurgitate. Three people performed these procedures (KT, BK, SJ). All birds were released within 10 minutes.

Food samples were obtained by administering tartar emetic following method by Poulin et al. (Poulin et al. 1994b; Poulin et al. 1994c; Poulin and Lefebvre 1995). Immediately after capture, birds were given 0.8 cm^3 of 1.5% antimony potassium tartar per 100g of body mass. We lowered the concentration from 1.5% to 1.0% for birds smaller than 10 g according to recommendations (Poulin and Lefebvre 1995). The solution was given orally through a flexible plastic tube attached to a 1-cc syringe. After administration, the birds were placed in a special “regurgit-bowl” covered by dark cloth. The bowl formed the base and the cloth formed a bag that was accessible from the upper part (similar way to classical mist-netting bags. This allowed us to handle birds quickly and safely. The bottom of “regurgit-bowl” was cleaned with water and detergent, and toilet tissue after each bird. Regurgitated food items were preserved in absolute ethanol. Weak individuals found in the net and breeding females were not used for the study. All individuals were sampled only once, and were released immediately after recapture.

We (KT, JS) examined each food sample (defined as regurgitated food of a single bird individual) under a dissecting scope. The number of arthropod individuals per morphospecies was assembled from body parts found in the sample (minimal number of individuals rule). Most of the arthropods were fragmented, and their identification was thus based on the least digestible and most characteristic parts (guide available online http://tvardikova.weebly.com/downloads.html). Individual arthropods were identified to morphospecies (i.e., morphologically identical prey categories assumed to represent one species), and classified to orders or families where possible. Further analyzes were also based on the classification of arthropods into the higher taxa listed in Table 3. We used published information (Tatner 1983; Ralph et al. 1985), and the insect collections of our team as reference. We measured the length of each arthropod individual or body part to the nearest 0.1 mm. We estimated the body length according to the published order-specific equations using the lengths of different body parts (Calvemr and Woolledd 1982; Diaz and Diaz 1990; Hodar 1997). We used body length to estimate body weight for arthropods according to Ganihar (1997). Presence or absence of nectar, and its relative volume in sample, was evaluated through the presence of pollen grains using microscope. Similarly, percentage of plant material was estimated from the length or volume of plant parts.

We classified bird species represented by more than four samples into feeding guilds by cluster analysis (using abundances of arthropod taxa listed in Table 3, average linkage clustering in package vegan, function hclust (R Development Core Team 2009). Root (1967) defined a guild as a group of species that exploits the same class of environmental resources in a similar way. We defined guilds as groups of species that feed on the same food (arthropods, fruits + seeds, nectar) in similar proportions (Simberloff and Dayan 1991; Poulin et al. 1994b).

Each food sample contained the remains of food eaten over an unspecified time span, and as such does not represent the complete diversity of food items taken. We calculated food specialization using the Brillouin diversity index (H) according to Sherry (1984), and examined the accumulation curves for all species.

RESULTS

We forced 999 birds to regurgitate and our data set comprised 99 species occurring at 10 different sites. Eighty-five (8.5 %) regurgitated samples included liquid only and 175 birds (17.5%) failed to regurgitate. We thus analyzed 739 food samples from 99 bird species, and identified 3,504 food items (i.e. arthropod individuals, seeds or other plant materials), from which 2,728 items were arthropods (Table S1 SuppInfo.pdf). Overall, 77 bird species were represented by more than four food samples, (36 species were represented by 4 - 5 samples, and 41 bird species by more >6 samples; Table S2 SuppInfo.pdf) and used in the subsequent analyzes. Data from the lowland site Wanang were combined with the 200 m a.s.l. altitudinal gradient site for the analyzes of prey abundances, importance and size along altitudinal gradient, as they did not differ significantly in measured parameters (arthropod body size: SS = 12.03, df = 5, MS = 1.71, *F* = 1.67, *P* = 0.12, avian body size SS = 0.41, df = 5, MS = 0.08, *F* = 0.86, *P* = 0.51). Similarly, data from Kotet were combined with the Mt. Wilhelm 1700 m a.s.l. data (arthropod body size: SS = 0.01, df = 1, MS = 0.01, *F* = 0.26, *P* = 0.61, avian body size SS = 0.13, df = 1, MS = 0.13, *F* = 0.15, *P* = 0.70).

The cluster analysis identified all 715 food samples into four groups which we arbitrary recognized as food samples belonging to nectarivores-insectivores (Ne-In), frugivores- insectivores (Fr-In), insectivores (In), and frugivores (Fr). All species were identified into one of these feeding guilds (Table 1, Fig. S1 SuppInfo.pdf) based on this analysis. We compared our field data with information from the literature (Hoyo et al. 1992-2011). The proportion of insectivores decreased from 75% of all species, based on data from the literature, to 42% based on our data, as many presumably insectivorous species also fed partly on fruits or nectar. On the other hand, the number of species reported to feed on insect and fruits increased from 6.5%, based on data from literature, to 40% based on our data (Fig. 1).

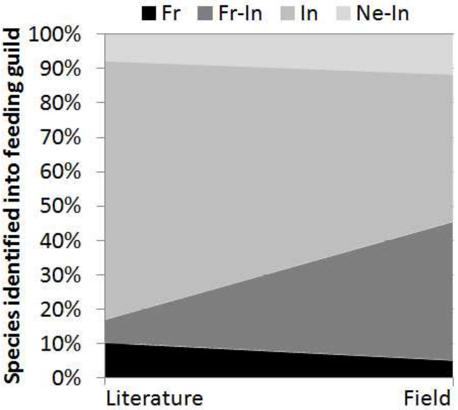

Figure 1. Available data published tend to underestimate plant components (fruits, nectar) in the diet of insectivorous birds

Birds eating (or samples including) almost exclusively arthropods (99%) were classified as insectivores (or sample belonging to insectivorous bird respectively), birds consuming 55 - 85% of arthropods and 25 - 48% fruit parts were classified as frugivores-insectivores; birds feeding mainly on fruits (98%) were classified as frugivores and birds consuming nectar and fruits or nectar and insects were classified as nectarivores (Table 2, Table S2 SuppInfo.pdf). The mean proportion of each food type in the diet differed among the feeding guilds, although the standard deviation of the mean was rather high in some cases (Table 2). We compared our data with available information on food specialization extracted from literature, and found differences in 27 species (Table 1).

Nine species (*Toxorhamphus novaeguineae*, *Toxorhamphus poliopterus*, *Oreocharis arfaki*, *Melidectes princeps*, *Oedistoma iliolophus*, *Myzomela rosenbergii*, *Melidectes fuscus*, *Micropsitta pusio*, *Melilestes megarhynchus*) of the 77 species studied were recognized as insectivores-nectarivores by cluster analysis. We did not find any species taking nectar only (*Myzomela rosenbergii* was the most nectarivorous species observed), as most individuals of the species classified as nectarivores fed extensively on small, soft-bodied arthropods and fleshy fruits together with nectar. Many small insectivorous-frugivorous species fed on a large diversity of plant species and plant parts, as well as arthropod taxa (as in Table 3).

Species of genus *Melanocharis* and *Peneothello* fed most extensively on fruits (Table 1, Table S2 SuppInfo.pdf). On the other hand, *Crateroscelis robusta*, *Microeca papuana* and genus *Pachycephla* were characterized by a lower intake of fruits and seeds (Table 1, Table S2 SuppInfo.pdf) compared to other mixed-feeders.

Table 1. Classification of bird species into feeding guilds, and number of samples from individual birds in each species species identified into feeding guilds according to cluster analysis. Bird species represented by ≥4 food samples (n = 77 bird species) are included, and their feeding specialization is compared to information extracted from literature (Hoyo et al. 1992-2011). Bird species where our data on food differ from the information extracted from literature are marked by asterisk. Fr = Frugivores, In = Insectivores, Fr-In = Frugivores-insectivores, Ne-In = Nectarivores - insectivores. See tables S1 and S2. in Supplementary Information for details on food items taken.

Species	Food according to literature		Number of samples identified into feeding guild acording to our data					Species feeding guild
	Primary	Secondary	Fr	In	Fr-In	Ne-In	Total	
Acanthiza murina	In	Ne		1	2	1	4	Fr-In
Alcedo azurea	In	Ca		10			10	In
Aleadryas rufinucha	In			4			4	In
*Amalocichla incerta**	In			4	2	1	7	Fr-In
*Arses insularis**	In			1	4		5	Fr-In
Ceyx lepidus	In			3	1		4	In
Clytomyias insignis	In			3	1		4	In
Colluricincla megarhyncha	In		3	10	3	1	17	In
Coracina melas	In			3	1		4	In
*Coracina montana**	Fr	In		8	2		10	In
Crateroscelis murina	In			8	3		11	In
*Crateroscelis robusta**	In		3	9	9	1	22	Fr-In
Dacelo gaudichaud	In	Ca		4			4	In
*Gallicolumba beccarii**	Fr				4		4	Fr-In
Garritornis isidorei	In			10			10	In
Gerygone chrysogaster	In			3	1		4	In
Chalcophaps stephani	Fr		5				5	Fr
Ifrita kowaldi	In			4			4	In
Lonchura tristissima	Fr		3		1		4	Fr
Melanocharis nigra	Fr	In	7	7	5	1	20	Fr-In
Melanocharis striativentris	Fr		6		3		9	Fr
Melanocharis versteri	Fr	In	12	3	19	1	35	Fr-In
*Melidectes belfordi**	In				4		4	Fr-In
*Melidectes fuscus**	In			3	8	3	14	Ne-In
*Melidectes princeps**	Ne	In		8		5	13	Ne-In
Melilestes megarhynchus	In	Ne		3	1	1	5	Ne-In
*Meliphaga analoga**	In	Fr	5	4	8	1	18	Fr-In
*Melipotes fumigatus**	In		2	2	4		8	Fr-In
*Microeca papuana**	In			6	5		11	Fr-In
Micropsitta pusio	Fr	Ne				10	10	Ne-In
Monarcha axillaris	In			4	2		6	In
*Monarcha guttula**	In			9	5		14	Fr-In
Monarcha manadensis	In			3	1		4	In
Myiagra alecto	In	Fr		9	1		10	In
Myzomela rosenbergii	Ne	In		1		3	4	Ne-In
Oedistoma iliolophus	In	Ne		2	1	1	4	Ne-In
*Pachycephala hyperythra**	In			3	5		8	Fr-In
Pachycephala modesta	In			3	1		4	In

*Pachycephala schlegelii**	In			6	10		16	Fr-In
*Pachycephala simplex**	In			3	1		4	Fr-In
*Pachycephala soror**	In			1	2		4	Fr-In
Pachycephalopsis poliosoma	In			10			10	In
Paramythia montium	Fr		9		4		13	Fr
Peneothello bimaculata	In			8	2		10	In
*Peneothello cyanus**	In			8	14		22	Fr-In
Peneothello sigillata	In	Fr		7	13		20	Fr-In
Pitohui dichrous	Fr	In			4		4	Fr-In
*Pitohui kirhocephalus**	In	Fr		10			10	In
*Pitohui nigrescens**	In	Fr		10			10	In
*Poecilodryas albispecularis**	In			2	4		6	Fr-In
Poecilodryas hypoleuca	In			3	1		4	In
Ptiloprora guisei	In	Fr		2	2		4	Fr-In
Ptiloprora perstriata	In	Fr	4	9	10	2	25	Fr-In
Ptiloris magnificus	Fr	In		2	4		6	Fr-In
Ptilorrhoa caerulescens	In			10			10	In
*Rhagologus leucostigma**	Fr		1	1	7		9	Fr-In
Rhipidura albolimbata	In			14	2		16	In
Rhipidura atra	In			30	4		34	In
*Rhipidura brachyrhyncha**	In			3	3		6	Fr-In
Rhipidura rufidorsa	In			10			10	In
Rhipidura rufiventris	In			4			4	In
Rhipidura threnothorax	In			3	1		4	In
Sericornis arfakianus	In			4			4	In
*Sericornis nouhuysi**	In			6	12		18	Fr-In
*Sericornis papuensis**	In			2	6		8	Fr-In
*Sericornis perspicillatus**	In			9	13		22	Fr-In
Sericornis spilodera	In			1	3		4	In
Sericornis virgatus	In			3	1		4	In
Syma torotoro	In			10			10	In
Tanysiptera galatea	In			8			8	In
Toxorhamphus novaeguineae	In	Ne	2	7	1	1	11	Ne-In
Toxorhamphus poliopterus	In	Ne		2	2	1	5	Ne-In
Tregellasia leucops	In	Fr		2	2		4	Fr-In
Turdus poliocephalus	In	Fr	2	1	2		5	Fr-In
Xanthotis polygrammus	Ne	Fr	2		1	2	5	Ne-In
Zoothera heinei	In	Fr		2	2		4	Fr-In
Zosterops novaeguineae	In	Fr		3	1		4	In
		Total	66	371	241	36	715	

Table 2. Representation of different food types in the diet of bird species from different guilds. Mean proportion of items from each food type found in the samples is given for species from different feeding guilds (N = 77 bird species).

Feeding guilds	Arthropods	Fruit/Seeds	Nectar
Nectarivores-Insectivores (N = 9)	35.78±5.6	15.69±1.7	48.53±26.2
Frugivores (N = 4)	1.57±0.5	98.10±0.2	0.0
Frugivores-insectivores (N = 31)	70.09±14.9	35.55±1.5	0.46±4.0
Insectivores (N = 33)	97.47±1.9	3.53±0.1	0.00

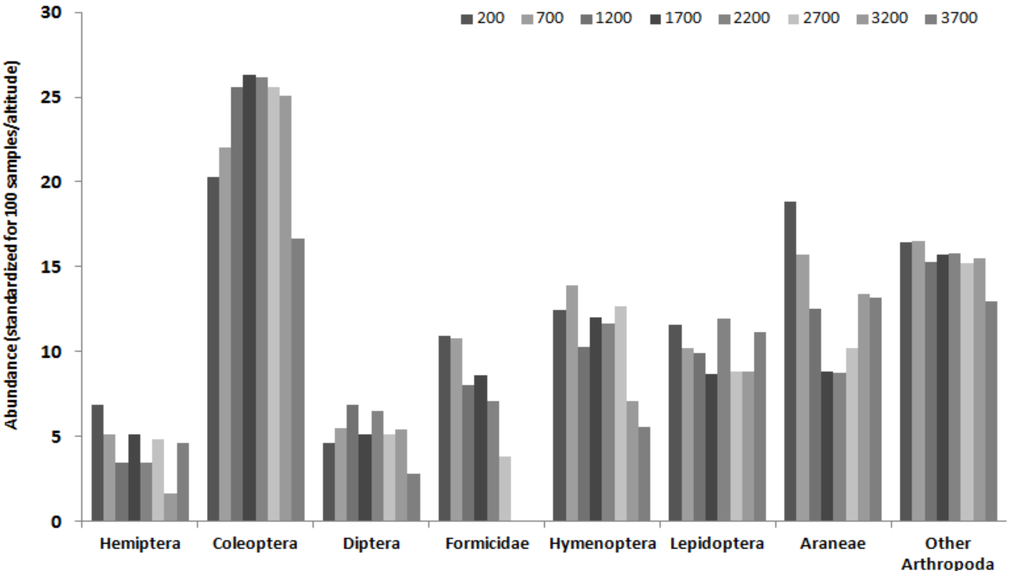

Figure 2. Abundance of arthropod groups found in food samples at 10 altitudinal sites. Abundance standardized per 50 samples selected randomly across all bird species at each altitudinal site. Samples from Kotet included in site 1700 m a.s.l., and Wanang in 200 m a.s.l.

Insectivores usually fed on a large variety of arthropods, and we did not observe any differences in relative representation of insect taxa in the diet among bird species, except that *Rhipiduridae* tend to take more individuals of ants than other bird species occurring at the same study sites.

Food exploitation

Coleoptera was the best represented arthropod taxa (based on Table 3), being found in the diet of 90 bird species, followed by Araneae (81 species), Hymenoptera (80 species), and larval Lepidoptera (64 species; Table 3, Table S2 SuppInfo.pdf and Fig. 2). Most sampled bird species fed on several (mean = 6.3, Fig. 3) invertebrate taxa, but Coleoptera were most frequent. These four invertebrate taxa alone accounted for 67% of all invertebrate items found in all food samples. We recorded 713 individuals of Coleoptera, 399 individuals of Araneae and 365 individuals of Lepidoptera (103 adults vs. 262 larvae) in 2,728 individuals of described invertebrates. Hymenoptera (469 individuals) were also very common in the food samples. Bees and wasps were represented by only a few individuals, whilst ants were found in many food samples (201 ant individuals in 153 samples). The abundance of ants in food samples decreased with altitude, and ants were not present in food samples from 3200 and 3700 m a.s.l. (Fig. 2).

Table 3. The importance of different invertebrate taxa in the birds' diet quantified as the number of items (i.e., individual body fragments) and species from various taxa, and the number of samples (each from one individual bird) where they were present. First (and second) choice within arthropod taxa was identified as taxa presented by maximum (and second maximum) number of individuals, but only if this value is higher than 2*Mean number of individuals per invertebrate taxon.

	Invertebrates			Number of bird species		
	Number of individuals	Number of samples with taxa present	Individuls/Sample	taking taxon	taking taxon as first choice	taking taxon as second choice
Araneae	399	291	1.37	81	8	2
Chilopoda	17	9	1.89	11		
Coleoptera	713	430	1.66	90	25	10
Dermaptera	21	17	1.24	17		
Diplopoda	9	5	1.80	6		
Diptera	137	100	1.37	53		
Gastropoda	15	9	1.67	10		
Neuroptera	24	26	0.92	15		
Odonata	16	15	1.07	7		
Orthoptera	40	35	1.14	22		1
Ricinulei	11	11	1.00	11		
Hemiptera	141	174	0.81	51	2	2
Lepidoptera adult	103	126	0.82	41		1
Lepidoptera larvae	262	202	1.30	64	3	3
Hymenoptera: ants	201	153	1.31	62	1	1
Hymenoptera: others	249	170	1.46	63	2	1
Hymenoptera: bees	6	5	1.20	5		
Hymenoptera: wasps	13	10	1.30	10		
Insect egg	189	87	2.17	47	3	1
Insect larvae	24	22	1.09	13		
Insect pupae	138	92	1.50	24	1	2
Total	2728					

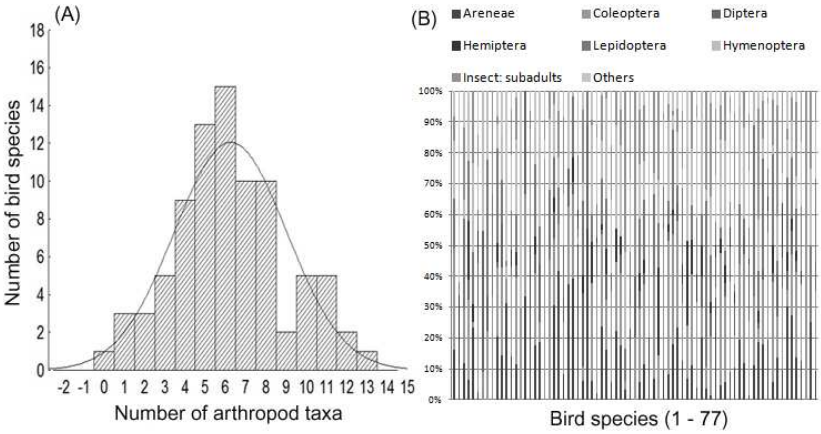

Figure 3. Average number of arthropod taxa taken by bird species (A) and proportional abundance of arthropod taxa in food samples of birds represented by more than four samples (B).

Most of the birds also fed on vegetable material. Only five of the 77 species analyzed did not have any plant material in food samples, including three kingfishers (*Alcedo azurea*, *Dacelo gaudichaud*, *Syma torotoro*), and *Coracina montana* and *Rhipidura rufidorsa*. The proportion (% of sample volume) of plant material in food samples increased with altitude (y = 3.0*x + 15.19, $R^2 = 0.06$, $F_{1,556} = 16.67$, $P < 0.001$; Fig. 1) and the proportion of arthropods in food samples decrease accordingly (y = -1.62*x + 35.64, $R^2 = 0.08$, $F_{1,556} = 4.49$, $P = 0.03$; Fig. 4). The abundance of some taxa (Hemiptera and Lepidoptera) in food samples was constant across all altitudes, other decreased nearly linearly with altitude (Formicidae, Hymenoptera), whilst for other taxa there did not appear to be a simple linear relationship between abundance and altitude. The Coleoptera and Diptera are a case in point, with the abundance appearing to have hump-shaped distribution along altitudinal gradient (Fig. 2).

Variation, heterogeneity and patchiness

We explained most of the variability in food items in samples by bird species, furthermore our cluster analysis grouped most of the samples from one bird species together. Cluster analysis, run for samples of the four most common species (*Colluricincla megarhyncha*, *Crateroscelis robusta*, *Melanocharis versteri* and *Sericornis perspicillatus*, Fig. S2 SuppInfo.pdf) collected at different sites showed that species were largely clustered together, with some exceptions. In three species we could analyze samples from at least three different altitudes. In two of these species, the diet from adjacent altitudes was more similar than from attitudinally more distant sites (Fig.S2 SuppInfo.pdf).

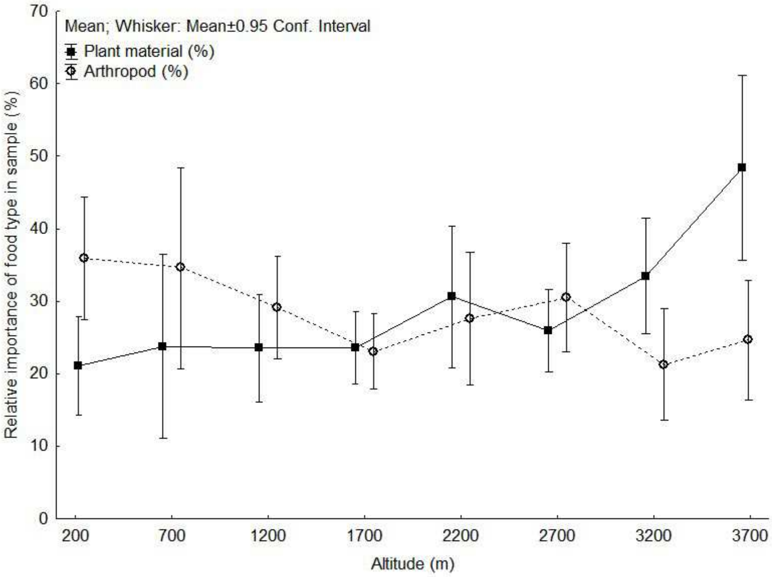

Figure 4. Relative importance of arthropods and plant material in individual food samples along altitudinal gradient. Samples from Kotet included in site 1700 m a.s.l., and from Wanang in 200 m a.s.l.

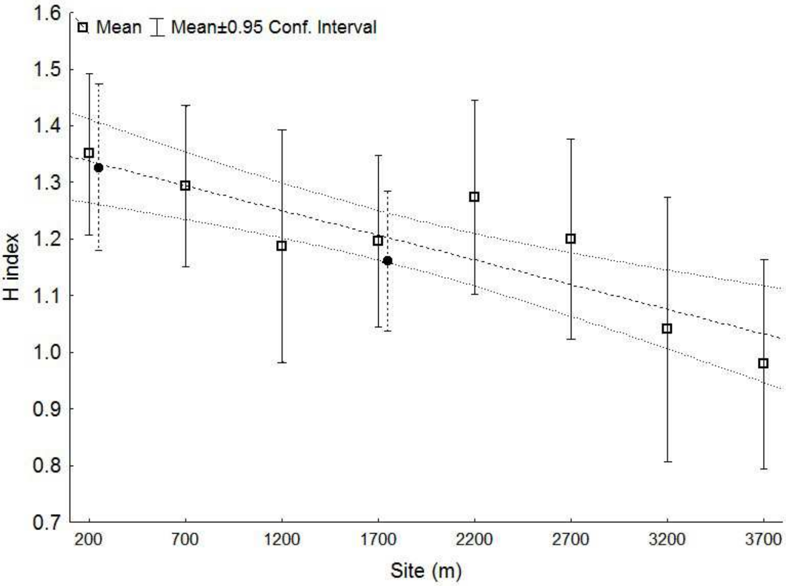

Figure 5. Brillouin diversity index (H) of invertebrate species in the diet of insectivorous bird species along Mt. Wilhelm altitudinal gradient and in Kotet (dotted line at 1700 m a.s.l.) and Wanang (dotted line at 200 m a.s.l.).

Diet varied considerably among conspecific individuals, and more samples would be necessary to describe food exploitation by individual species at each site for 4 of the 6 species analyzed (based on the cumulative curves of morphotypes recorded per sample and comparison with Chao2 estimates) whereas 10 samples were sufficient to describe arthropod exploitation by other species (e.g. *Melanocharis nigra, Melanocharis versteri;* Fig. S2 SuppInfo.pdf). The overall diversity of food items in the diet of bird species decreased with altitude (Mean H = 1.3925-0.0449*Altitude, P = 0.33, F = 2.23; Fig. 5).

The majority of taxa (listed in Table 3) comprised just one prey item per morphospecies, including 0.9-1.5 morphospecies per taxon in one food sample in average. On average 69.2% of morphotypes in each sample (mean per sample ± SD = 6.30 ± 3.26) were represented by singletons. Predominance of singleton morphospecies was particularly frequent in large invertebrates (millipedes, centipedes, dragonflies and cicadas). Berger-Parker index had a log-normal distribution (Mean ± SD = 0.26 ± 0.19), with most of the dominant species being represented by the most abundant species. Approximately 3% of the samples contained between 7 - 13 individuals per morphospecies (Berger-Parker > 0.88), suggesting that those bird species were either feeding within true clumps of prey species, or selectively feeding on particular prey that a bird repeatedly encountered. Those samples were quite large (more than 20 insect individuals in each sample), came from between 200 - 1200m a.s.l., and were dominated by *Formicidae*, Coleoptera or insect larvae. *Formicidae* were presented in average by 2.2 morphospecies per sample, and Coleoptera by 1.9-2 morphospecies per sample, and insect larvae and pupae with 2.1 morphospecies per sample. *Melanocharis versteri*, *Peneothello sigillata* and *Crateroscelis robusta* were found with few morphospecies of *Curculionidae* beetles per samples. *Crateroscelis murina*, *Sericornis papuensis, Poecilodryas hypoleuca, Rhipidura threnothorax* took ant larvae in some patches. *Rhipidura atra* and *Rhipidura albolimbata* usually ate more adult ants of one morphotype.

Arthropods in bird diet along altitudinal gradient

We obtained body length, extrapolated to body weight (Ganihar 1997), for 1,538 arthropods taken by 62 bird species from all 10 sites (n = 185 - 123 arthropods/site). Mean body size of all arthropods from food samples decreased with altitude [Mean arthropod weight (log mg) = -0.0001* Altitude (m) + 0.1567; R^2 = 0.71, $F_{1,8}$ = 17.67, P = 0.03] but did not show any trend for the lower four altitudes (200m – 1700 m a.s.l.).

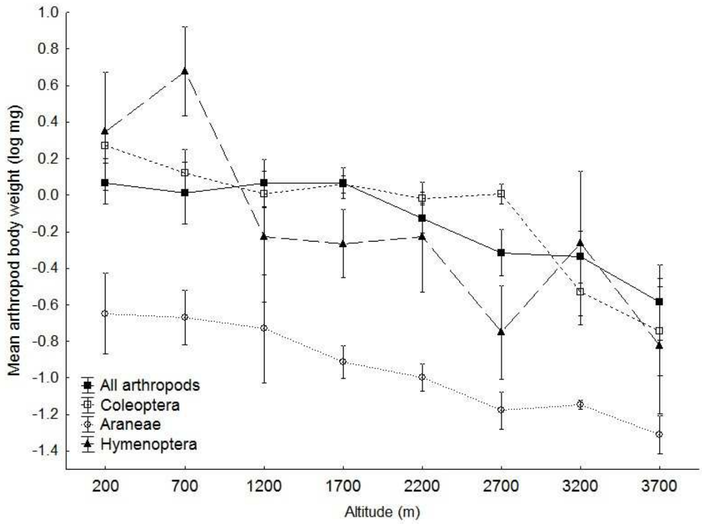

Figure 6. Altitudinal trends in mean (across all samples for altitude) body weight in the three arthropod orders that showed significant change in body weight with altitude and for all arthropods combined. Coleoptera : y = -0.0002x + 0.349 (*n* = 189, *t* = 6.06, R^2 = 0.20, *F* = 47.73, *P* < 0.001); Araneae: y = -0.0002x - 0.548 (*n* = 134, R^2 = 0.19, *F* = 17.98, *P* < 0.001), Hymenoptera: y = -0.0004x + 0.530 (*n* = 123, R^2 = 0.11, *F* = 10.73, *P* = 0.001); All arthropods: y = -0.0002x + 0.1933 (*n* = 530, R^2 = 0.02, *F* = 11.14, *P* < 0.001). Samples from Mt. Wilhelm (all altitudes), Kotet (1700 m) and Wanang (200 m). The Kotet and Wanang samples were combined with sites from the corresponding altitude at Mt. Wilhelm.

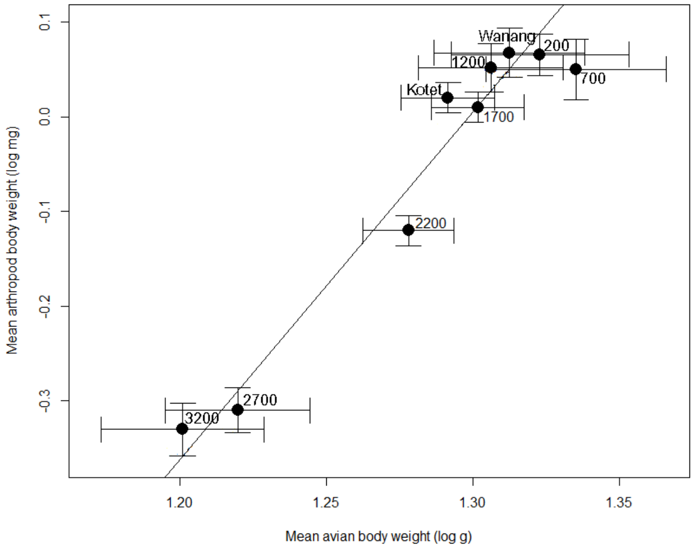

Figure 7. Relationships between mean body weight of bird individuals and arthropod prey in their individual food samples. Each point represents one bird community, either from a particular altitude at Mt. Wilhelm, or from Kotet (1700 m) and Wanang (200 m). Mean arthropod weight = 3.399*Mean avian weight - 0.241, R^2 = 0.94, *P* < 0.001, $F_{1,7}$ = 69.87

The trend was caused mainly by body weights of Araneae, Coleoptera and Hymenoptera (without Formicidae) whose body weights decreased significantly with increasing altitude when we tested individual arthropods orders separately (Fig. 6). Other orders (Neuroptera, Hemiptera and Diptera) did not show any trend, did not occur in samples at higher altitudes (ants), or occurred only scarcely in samples (n < 100 individuals, or n < 5 individual/site).

The mean body weight of insectivorous bird species declined with increasing altitude from 21.03 g at 200 m a.s.l. to 15.88 g at 3200m a.s.l., and 21.1 g at 3700 m a.s.l. [Mean bird weight (log g) = -0.0004*Altitude (m) + 1.342, $R^2 = 0.86$, $F_{1,8} = 43.21$, $P < 0.001$]. Finally, the mean weight of insectivorous birds and their insect prey were correlated between altitudes 200 – 3200 m asl. ($n = 9$, $R^2 = 0.91$, $F_{1,7} = 67.83$, $P < 0.001$, Fig. 7). Inclusion of the data from 3700m asl. made the correlation non-significant ($n = 10$, $R^2 = 0.18$, $F_{1,7} = 1.13$, $P = 0.33$). The body weight of all mist-netted birds also correlated with the size of food items taken ($n = 1538$, $R^2 = 0.04$, $F_{1,1536} = 44.27$, $P < 0.001$). There was no significant correlation ($p > 0.05$) between food items and size of individual bird species (n = 23 species with individuals mist-netted at 3 and more altitudes), however 10 species (e.g. both males and females *Melanocharis nigra, Alcedo azurea*) had bigger individuals at altitudes separated by 1000m altitudinal

DISCUSSION

This study is the first to have tested regurgitation methods in birds from Papua New Guinea and found it successful, reasonably harmless, and easy to use in field conditions. However, the dosage and concentration of administered emetic are very important (Lederer and Crane 1978). We based our doses on the method and recommendations published elsewhere (Tomback 1975; Poulin et al. 1994c; Poulin and Lefebvre 1995). Our chosen method appeared to provide good results with minimum damage to the birds. Bird mortality was only 0.5% (i.e., two individual deaths during handling). Birds smaller than 5 g do not occur in Papua New Guinea; our results are therefore not relevant to the use of emetic tartar in such small birds. We did not observe any significant differences in mark-recapture rates between sites when emetics were used and those at which they were not.

The number of food samples needed to represent the diet of a species at one locality depends mostly on the number of items per sample, the diversity of prey types taken by species, and the heterogeneity of food samples from different individuals. All these parameters varied among the species studied, and more (usually more than 10) food samples were needed to record the diversity of prey types that some species eat. Based on this knowledge and the material available, we compromised and used only species represented by more than four food samples in our analyses. Incompleteness of the information on food item variability has to be taken into account when we interpret the results. The data presented here represent food taken by mist-netted birds only, i.e. those occurring and foraging mostly in understory and mid-story of tropical forests, but not those concentrated in the forest canopy. However, our data from 99 bird species represents a large proportion of entire bird communities, including 257 bird species across all study sites (KT, unpublished data).

Our results suggest that the regurgitation method is useful for determining the diet of terrestrial birds with a variety of feeding specializations. Information on bird diets is largely missing from literature, as only a few quantitative data sets reporting the relative importance of arthropods, nectar and fruits in the diets of tropical birds exist (Collins et al. 1990). Most insectivorous species occurring at our study sites fed on a variety of arthropod taxa, suggesting that dietary specialization of insectivores was not prevalent in tropical habitats. Many tropical bird species were assumed to be food specialists (Poulin et al. 1994a); however other studies from various tropical habitats have reported birds to be opportunistic (Kaspari and Joern 1993). A variety of models based on short-term diet optimization have predicted that organisms should broaden their diets during periods of food scarcity and narrow them, using the most rewarding food, when food is abundant (review in Pyke et al. 1977). Chronically low arthropod abundance within the rainforest interior (Basset et al. 1992; Novotny et al. 2006) may therefore require broad diets for some birds to persist there. The current study supports the hypothesis that birds are mainly opportunists: consuming prey in proportion to its relative abundance in habitat.

The fact that beetles were the most abundant food item followed by spiders, Hymenoptera and caterpillars reflects diet opportunism and the situation in tropical forest, where these three groups were most abundant (Basset et al. 2012). In contrast, other studies have found Hymenoptera to be nearly as abundant as Coleoptera (Lamarre et al. 2012). Coleoptera was the most abundant taxon caught by flight intercept traps in Lamington National Park in Australia followed by Diptera, Hymenoptera and Araneae (Boulter et al. 2011). Coleoptera was also the most abundant arthropod taxon (followed by spiders and caterpillars) found on mid-story and under-story growth in our lowland site (Tvardikova - unpublished data obtained by complete quantitative collection of arthropods from 20 3 - 4 m high saplings, which were cut down in Wanang site), where most of the sampled bird species presumably hunt. Slightly different relative abundances were found in the canopy of ten fogged lowland Bornean trees where Diptera was the most abundant taxon followed by *Formicidae*, Coleoptera, Hemiptera, Hymenoptera and Arachnida (Stork and

Blackburn 1993). Our results on abundances of arthropod taxa in food samples are similar to findings from Venezuela (Poulin et al. 1994a) and Australia (Razeng and Watson 2012). The predominance of beetles, spiders, and caterpillars also suggests that most bird species foraged by gleaning, and that is what we observed during our surveys. Therefore, the lower abundances of flying insects (Diptera, Hymenoptera) found in food samples do not have to reflect their abundance in rain forest.

The most well studied bird species differed in the variety and proportion of insect morphospecies in their diet, despite the opportunism observed for bird species in general. This allowed us to assign species into feeding guilds by a cluster analysis based on the proportion of the different food types found in their regurgitated samples. Our results for the most abundant species sampled from 10 sites show that variability in food items taken can be explained by bird species. Relatively low variability within bird species food samples is likely determined by micro-habitat (i.e. substrate, forest strata), where birds forage and bird species specific foraging techniques. However some spatial differences do occur. Birds of the same species from different localities tend to fall into the same cluster, which shows that individual species tend to take same proportion of different food items at different sites. This may be due to conservation of the foraging techniques used by birds, which seems to be a function of the morphological and perceptual traits of each species. Robinson and Holmes (1982) demonstrated a relationship between the search tactics used by birds foraging for insects among forest foliage and the kinds of prey captured. Yet these behaviours are not totally fixed or stereotyped. The foraging tactics of some species are known to vary between habitats, between sexes and even from one year to another within the same habitat (Morse 1971; Robinson and Holmes 1982; Cale 1994; Morse 2008). A different approach (Ricklefs 2012) to feeding specialization shows that passerine birds are clustered toward the centre of their morphological space, and most species seem to have a generalized morphology suited to a variety of foraging substrates and movements, as well as prey items.

Indeed, we found food exploitation to be quite variable within many species with, most of the arthropod morphospecies found being represented by a single food item in each sample. This result leads us to the conclusion that most birds sampled in this study forage opportunistically, rather than concentrating on a particular prey species. This pattern is particularly striking considering that arthropod species are often aggregated in tropical forests (Basset 2001). The morphospecies accounting for the highest aggregation in food samples were morphospecies of Hymenoptera, especially wasps, ants, and ant eggs. Not a single bird species seems to be specialized on particular taxa, except *Rhipiduridae* that fed on ants and *Curculionidae* more often than other bird species. Some curculonid beetles found in our samples in many morphotypes (mainly *Zygopinae, Cryptorrhynchinae*) are reported to occur in higher aggregations in tropical forests (Dyer et al. 2012). We believe that this pattern resulted from feeding on aggregations of these species in time in our sites, and not from specialization of birds. The presence of ants in food samples reflects the distribution of ants along altitudinal gradients, and their steep decrease in abundances with altitude (Boulter et al. 2011; Yusah et al. 2012). Based on pitfall trapping (Fayle and Moses, unpubl. data) and tuna baits (Tvardikova and Moses, unpubl.data), ants were highly abundant at low altitudes but became scarce at 2200 m a.s.l. and reached the upper limit of their distribution at 2700 m a.s.l. Birds feeding on ants were observed to search mainly on the ground, and in the understory. This corresponds to the presence of ant workers (95 %) in food samples, while reproductive stages of ants (5%) were nearly missing. Our observation corresponds with findings of Sherry (1984), who used frequencies of aerial vs. non-aerial foraging tactics to determine whether flying (reproductive) or non-flying (primarily worker) ants were eaten by Neotropical Flycatchers.

Most of the frugivorous species also included arthropods in their diets, several typically insectivorous species fed at least occasionally on fruits. We recorded partial frugivory or extensive intake of fruits for some birds species previously considered to take insects only (*Crateroscelis robusta, Crateroscelis murina, Gerygone chrysogaster, Ifrita kowaldi, Microeca papuana, Monarcha axillaris, Pachycephala hyperythra, Pachycephala Schlegelii, Peneothello bimaculata* and *Peocylodrias albispecularis*). On the other hand, we also recorded insects in a few samples of bird species considered fully frugivorous (*Cnemophylus macgregorii, Melanocharis striativentris, Paramythia montinum, Rhagologus leucostigma*). Overall, the diversity of food items decreased with altitude, and the proportion of species feeding upon plant items became larger. We believe that this trend reflects general decrease in the diversity and abundance of arthropods with increasing altitude (Olson 1994; Guevara and Aviles 2007; Larsen et al. 2011). Orians (1969) found that certain insectivorous specialists disappeared with increasing altitude, as the diversity and abundance of some insect groups decreased, and birds could not specialize on them. Several major groups including ants and termites disappear altogether above 2,500 m, while others (larval Lepidoptera, Orthoptera, Diptera, Coleoptera, Hymenoptera) are notable for their rarity at higher altitudes (Terborgh 1977).

Mean body size of insectivorous species decreased with increasing altitude on Mt. Wilhelm, and correlated positively with mean body size of arthropods decreasing towards cooler and higher altitudes. A general decrease in the mean size of species within insect communities with increasing altitude was observed in different arthropod taxa (Janzen et al. 1976; Guevara and Aviles 2007). The combination of all arthropod taxa sampled using different collecting techniques show that, on average, insects in the Ecuadorian lowland rain forest are larger than insects found in adjacent high-altitude cloud forest habitats (Hodkinson 2005). These results are comparable to three previous studies (Janzen et al. 1976; Powers and Avilés 2007) that also found a decrease in the average insect size at higher altitudes.

The body size of individual birds is correlated with the size of the insect taken. A similar pattern was previously (Janes 1994) suggested for avian guilds dependent directly or indirectly upon arthropods, but not for other guilds independent of arthropods. A general relationship between predator size and prey size has been observed among a variety of insectivorous birds dependent on free living insects (Hespenheide 1971; Janes 1994). Our data did not confirm the correlation between body size of bird and prey within individual bird species; however we recorded significantly heavier bird individuals in higher altitudes. We also observed relatively large bodied birds taking relatively small insects at the tree line (3700 m a.s.l.). None of those species is purely insectivorous, and most of them feed on nectar and fruits, and forage mainly in the forest canopy. Such a guild was generally missing from our mist-nets at lower altitudes, where nets do not reach to the top of canopy. At the same time, the large-bodied insects are rare at the tree line site, and small insects seem to be taken opportunistically together with nectar or fruits. We believe that those two facts explained the mismatch between bird and prey body sizes at 3700 m a.s.l.

Although an exact assessment of bird diet would be a difficult task, our study brings the first report on food preferences of birds from Papua-New Guinea using a non-destructive method. Our data are consistent with the hypothesis that most of the bird species feed opportunistically on wide range of food items. We show that the diversity of food items taken by birds decreases towards higher altitudes, and that the disappearance of some insect taxa as diet items corresponds with their disappearance from the available food resources. Our findings support the notion that the body-sizes of insectivores are to some extent determined by the insect size composition of their environments. To our knowledge, no previous study has detailed the food preference of variety of bird species along a complete altitudinal gradient.

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SUPPLEMENTARY MATERIAL

Table S1. Number of invertebrate individuals and fruits/seeds, and presence or absence of nectar found in food samples from all bird species surveyed (N = 99 bird species).

Table S2. Relative representation and diversity of different food types in the diet of individual bird species. Only species represented by ≥4 food samples are included (N = 77 birds, 715 food samples).

Figure S1. Cluster analysis of species according to their diet based on identification into higher taxa listed in Table 3.

Figure S2. Cluster diagram of diet composition for four common bird species (Colluricincla megarhyncha, Crateroscelis robusta, Melanocharis versteri and Sericornis perspicillatus) sampled at the altitude 200, 700, 1200, 2200, 2700, 3200, and 3700 m asl. of Mt Wilhelm altitudinal gradient and at 1700 m asl. in Kotet (1700K). Diet identification is based on identification into higher taxa listed in Table 3.

Figure S3. Randomised species accumulation curves for three selected species (with N ≥ 9 from the same altitude). Sample = regurgitated food from an individual bird.

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SUPPLEMENTARY MATERIAL

Table S1. Number of invertebrate individuals and fruits/seeds, and presence or absence of nectar found in food samples from all bird species surveyed (N = 99 bird species). Bird species with ≤ 3 samples are marked by asterisk; those birds are not included in main analyzes. The arthropod taxon identified as first and second choice is underlined. First (and second) choice within arthropod taxa was identified as the taxon presented by maximum (and second maximum) number of individuals, if this value was higher than 2*Mean number of individuals per taxon. Unidentified insect larvae, pupae and eggs were excluded from the count of the number of invertebrate taxa; Lepidoptera and Hymenoptera were considered each a single taxon, although they are further subdivided in the table. The following miscellaneous items are not included in the table: fish and small rodent fragments in the samples *of Ceyx lepidus* (n=3), and bones of lizards in the samples of *Colluricincla megarhyncha* (n = 3), *Peneothello cyanus* (n = 2), *Grallina bruijni* (n = 2), *Pitohui dichrous* (n = 1), *Pachycephala hyperythra* (n = 1), and *Tregellasia leucops* (n = 1). One sample of *Alcedo azurea* included a nearly complete crab specimen (*Brachyura*). Small stones were found in samples of many species taking larger insects and/or seeds (e.g. *Colluricincla megarhyncha*, *Ifrita kowaldi*, *Grallina bruijni*), and in samples from all surveyed kingfishers.

		Percentage of samples including			Number of invertebrate taxa
Species	Number of samples	Invertebrates	Plant material	Polen	
Acanthiza murina	4	75	50	25	8
Alcedo azurea	10	100			10
Aleadryas rufinucha	4	100	50		8
Amalocichla incerta	7	100	29	14	8
Arses insularis	5	100	80		6
Ceyx lepidus	4	75	25		11
Chalcophaps stephani	5	100	40		3
Clytomyias insignis	4	100	50		5
Colluricincla megarhyncha	17	88	40	18	11
Coracina melas	4	100	50		6
Coracina montana	10	100			7
Crateroscelis murina	11	100	38		11
Crateroscelis robusta	22	87	61	9	14
Dacelo gaudichaud	4	100			3
Gallicolumba beccarii	4	75	75		3
Garritornis isidorei	10	80	50		5
Gerygone chrysogaster	4	100	25		9
Ifrita kowaldi	4	100	75		9
Lonchura tristissima	4	25	75		
Melanocharis nigra	20	55	65	5	5
Melanocharis striativentris	9	33	100		4
Melanocharis versteri	35	57	83	3	10
Melidectes belfordi	4	75	100		7
Melidectes fuscus	14	84	65	14	6
Melidectes princeps	13	100		80	3
Melilestes megarhynchus	5	80	20	20	7
Meliphaga analoga	18	70	75	10	8
Melipotes fumigatus	8	50	100		5
Microeca papuana	11	100	45		12
Micropsitta pusio	10		100	80	
Monarcha axillaris	6	83	50		9

Continuation Table S1	Percentage of samples including				Number of invertebrate taxa
Species	Number of samples	Invertebrates	Plant material	Polen	
Monarcha guttula	14	84	49		11
Monarcha manadensis	4	90	25		8
Myiagra alecto	10	80	70		9
Myzomela rosenbergii	4	75		100	8
Oedistoma iliolophus	4	100	25	25	6
Pachycephala hyperythra	8	100	62		7
Pachycephala modesta	4	100	50		3
Pachycephala schlegelii	16	100	66		13
Pachycephala simplex	4	100	25		4
Pachycephala soror	4	75	50		5
Pachycephalopsis poliosoma	10	80	30		11
Paramythia montium	13	24	100		5
Peneothello bimaculata	10	100	50		12
Peneothello cyanus	22	100	64		11
Peneothello sigillata	20	100	65		13
Pitohui dichrous	4	100	75		8
Pitohui kirhocephalus	10	100	30		9
Pitohui nigrescens	10	100	30		7
Poecilodryas albispecularis	6	100	83		7
Poecilodryas hypoleuca	4	100	25		9
Ptiloprora guisei	4	75	50		6
Ptiloprora perstriata	25	80	56	40	14
Ptiloris magnificus	6	100	66		9
Ptilorrhoa caerulescens	10	50	50		8
Rhagologus leucostigma	9	91	77		10
Rhipidura albolimbata	16	100	37		11
Rhipidura atra	34	100	50		13
Rhipidura brachyrhyncha	6	100	50		11
Rhipidura rufidorsa	10	100			6
Rhipidura rufiventris	4	100	25		7
Rhipidura threnothorax	4	100	50		13
Sericornis arfakianus	4	100	25		5
Sericornis nouhuysi	18	100	66		12
Sericornis papuensis	8	100	75		9
Sericornis perspicillatus	22	100	67		11
Sericornis spilodera	4	100	50		9
Sericornis virgatus	4	75	25		8
Syma torotoro	10	100			6
Tanysiptera galatea	8	100	50		11
Toxorhamphus novaeguineae	11	81	36	36	10
Toxorhamphus poliopterus	5	100	40	40	10
Tregellasia leucops	4	100	75		9
Turdus poliocephalus	5		100		1
Xanthotis polygrammus	5		80	30	
Zoothera heinei	4	100	25		4
Zosterops novaeguineae	4	100	25		8

Table S2. Relative representation and diversity of different food types in the diet of individual bird species. Only species represented by ≥4 food samples are included (N = 77 birds, 715 food samples).

Bird Species	Number of samples	Number of invertebrate	Areneae	Chilopoda	Coleoptera	Dermaptera	Diplopoda	Diptera	Gastropoda	Neuroptera	Odonata	Orthoptera	Ricinulei	Hemiptera	Lepidoptera adult	Lepidoptera larvae	Hymenoptera: ants	Hymenoptera: others	Hymenoptera: bees	Hymenoptera: wasps	Insect:egg	Insect: larvae	Insect: pupae	Nectar	Fruit (+Seeds)	No. of invertebrates or fruits	No. of invertebrates or fruits in a sample
Acanthiza murina	4	5	2		4				1						1	1	3	2			1			Yes	2	17	4.25
Alcedo azurea	10	3	5	1		2	2		5	4	8	5		10		2										44	4.4
Aleadryas rufinucha	4	5	2		3					1			1		2	3		1			4				4	21	5.25
Amalocichla incerta	7	6	2		8			2	1					6		6		4		2				Yes	2	33	4.71
Arses insularis	5	4	4		2									1	3			5			4				4	23	4.6
*Cacomantis castaneiventris**	2		2		2											3	1					1				9	4.5
Ceyx lepidus	4	10	7		8			4			3	1		3		2	2	1	1		3				4	39	9.75
*Chaetorhynchus papuensis**	2				1			1						4	1	1	1				2					11	5.5
Chalcophaps stephani	5	3			2			1									1								26	30	6
Clytomyias insignis	4	5			2			1							1	3		2							1	10	2.5
Colluricincla megarhyncha	17	8	10		11			1	2		1	1		3		15	4				6		6	Yes	9	69	4.06
Coracina melas	4	5	1		2			1					1			1	1								1	8	2
Coracina montana	10	2	8		2					5	1	8					1				3					28	2.8
Crateroscelis murina	11	12	10	2	19		1	2				1		4		9	8	5			11				6	78	7.09
*Crateroscelis nigrorufa**	1		1					1						1	1	2		1			1			Yes		8	8
Crateroscelis robusta	22	11	15	2	37			5					1	6		16	17	13	1	1	3	6	9	Yes	15	147	6.68
Dacelo gaudichaud	4	1		5	3		2																			10	2.5
*Dicrurus bracteatus**	1		1		2										1	1					1					6	6
*Euaegotheles insignis**	1		1												1	1					1					4	4
*Eugerygone rubra**	1		1		1										1	1										4	4
*Eulacestoma nigropectus**	1				2									1												3	3
Gallicolumba beccarii	4	2	1		1			1																	24	27	6.75
*Gallicolumba rufigula**	1																								5	5	5
Garritornis isidorei	10	3	8		6							5				1		5							15	40	4
Gerygone chrysogaster	4	9	3	1	4			1				1		1		4	1	1							1	18	4.5
*Gerygone cinerea**	1		1		2									2				1								6	6
*Grallina bruijni**	1				1																				8	9	9
Ifrita kowaldi	4	10	3	1	10		2	3								2	1	2		1					4	29	7.25
*Lichenostomus obscurus**	2		1		2				1								1									5	2.5
Lonchura tristissima	4	1															1								17	18	4.5
*Melampitta lugubris**	1				4											3							2			9	9

Bird Species	Number of samples	Number of invertebrate	Areneae	Chilopoda	Coleoptera	Dermaptera	Diplopoda	Diptera	Gastropoda	Neuroptera	Odonata	Orthoptera	Ricinulei	Hemiptera	Lepidoptera adult	Lepidoptera larvae	Hymenoptera: ants	Hymenoptera: others	Hymenoptera: bees	Hymenoptera: wasps	Insect:egg	Insect: larvae	Insect: pupae	Nectar	Fruit (+Seeds)	No. of invertebrates or fruits	No. of invertebrates or fruits in a sample
Melanocharis nigra	20	6			25					1		2						2					2	Yes	58	90	4.5
*Melanocharis nigra**	1		5		6									1	3	3	3	2			6			Yes	26	55	55
Melanocharis striativentris	9	3			2											1		1			4				28	36	4
Melanocharis versteri	35	8	14		10			4						2	3	3	4	4			6		6	Yes	56	112	3.2
Melidectes belfordi	4	6	1		2			1		1						2		2			3				2	14	3.5
Melidectes fuscus	14	6	10		7			1						2		5		3						Yes	10	38	2.71
Melidectes princeps	13	2	5					3								1								Yes		29	2.23
Melilestes megarhynchus	5	7	17		4	1		1						2		6	6							Yes	5	42	8.4
Meliphaga analoga	18	5	14		5				1				1			4	2	1			5			Yes	40	73	4.06
*Meliphaga aruensis**	1													1								1		Yes		2	2
*Meliphaga montana**	1		1		7			4				1		1		4	1				4				3	6	6
Melipotes fumigatus	8	5	3		2			1									1		1						14	22	2.75
Microeca papuana	11	10	4		21	3	1				1	1		9		6	9	9		1	8				6	79	7.18
Micropsitta pusio	10																							Yes	24	24	2.4
Monarcha axillaris	6	6	3		7			2	1			1		3		2		4			6				3	32	5.33
*Monarcha frater**	1		1		1																1	1				4	4
Monarcha guttula	14	8	16		20			1			1			8	1	9	4	4			5		5		10	84	6
Monarcha manadensis	4	7	2		2			1						1		2	2	2			3				1	16	4
Myiagra alecto	10	7	1	1	5	2		1									2	1		1	3				3	20	2
*Myiagra cyanoleuca**	1		2		2									1			2	1			1					9	9
Myzomela rosenbergii	4	7	3		4			1					1	1			4	1			2			Yes		17	4.25
Oedistoma iliolophus	4	5	3		3											1	1	2			5			Yes	2	17	4.25
Pachycephala hyperythra	8	6	4		11			1								2	2	2			5				7	34	4.25
Pachycephala modesta	4	10	1		4			1		1				1		3	1	1		1	2	1			2	19	4.75
Pachycephala schlegelii	16	12	10		23	1		3		1		1	1	4	7	10	5	6					16		17	105	6.56
Pachycephala simplex	4	4	1		2												1	1							1	6	1.5
Pachycephala soror	4	4	1		5											4		1			4				3	18	4.5
Pachycephalopsis poliosoma	10	0			1			1													3				22	27	2.7
Paramythia montium	13	4			1									2		1		1			2				19	26	2
Peneothello bimaculata	10	11	4	1	19	1		6				1			4	6	7	1		1			6		6	63	6.3
Peneothello cyanus	22	8	6		31	1		2	1				1	2		5	8	10				4			18	89	4.05
Peneothello sigillata	20	11	17	1	35	1		6		1			1	2	1	24	1	3				1			13	107	5.35

Bird Species	Number of samples	Number of invertebrate	Areneae	Chilopoda	Coleoptera	Dermaptera	Diplopoda	Diptera	Gastropoda	Neuroptera	Odonata	Orthoptera	Ricinulei	Hemiptera	Lepidoptera adult	Lepidoptera larvae	Hymenoptera: ants	Hymenoptera: others	Hymenoptera: bees	Hymenoptera: wasps	Insect:egg	Insect: larvae	Insect: pupae	Nectar	Fruit (+Seeds)	No. of invertebrates or fruits	No. of invertebrates or fruits in a sample
*Philemon meyeri**	1		2		1																	4	1			8	8
Pitohui dichrous	4	5	4		6	1		1								1	3					1	2		6	25	6.25
Pitohui kirhocephalus	10	7	2		3			1				1		1	2	2	1						3		8	24	2.4
Pitohui nigrescens	10	1	2		5					2		2	1	8			9								9	38	3.8
Poecilodryas albispecularis	6	6	3		8									3		3	3	2			5				6	33	5.5
Poecilodryas hypoleuca	4	7	7		6					1				2	2	2	3	4			7				2	36	9
*Ptilinopus pulchellus**	1		1		1									1	1			1								5	5
Ptiloprora guisei	4	5	2		4											3		2			8	1			8	28	7
Ptiloprora perstriata	25	11	17		16	1		5				1	1	2	3	8	3	8	2	2	11			Yes	17	97	3.88
Ptiloris magnificus	6	8	3	1	5			2						1		4	1	4			8				10	39	6.5
Ptilorrhoa caerulescens	10	8	2		1	1		1						1		1	2		1						8	18	1.8
Rhagologus leucostigma	9	7	1		9	1								1	3	3	2	4			3		2		18	47	5.22
*Rhamphocharis crassirostris**	1				2			1																		3	3
Rhipidura albolimbata	16	8	5		24			4						5	2	2	6	24		1	3		11		6	93	5.81
Rhipidura atra	34	13	17	1	54	1		22				1		11	2	12	12	39		2			10		19	203	5.97
Rhipidura brachyrhyncha	6	7	3		3	1		3		1				1	7		3	4			3		6		3	38	6.33
*Rhipidura maculipectus**	1		1		3									1	1	1	4	1								12	12
Rhipidura rufidorsa	10	4	8		10							2			8		5	8								41	4.1
Rhipidura rufiventris	4	6	2		6			1							1		3	2			2				1	18	4.5
Rhipidura threnothorax	4	10	6		13	1		10		2		1		1	2	3	9	1			5		5		6	65	16.3
Sericornis arfakianus	4	4	1		2										2	3		1							3	12	3
Sericornis nouhuysi	18	9	10		22			1	1	1		1		2	2	5	2	7					19		12	85	4.72
Sericornis papuensis	8	8	6		7			1		1					7	5	1	1			4				6	39	4.88
Sericornis perspicillatus	22	11	20		36		1	7				1		5	2	7	4	18					2		19	122	5.55
Sericornis spilodera	4	7	2		11	1		1						3	4	6	1						5		3	37	9.25
Sericornis virgatus	4	8	3		3			3		1					1		2	1					8		1	23	5.75
Syma torotoro	10	5	1		3			1						2				1					3			11	1.1
Tanysiptera galatea	8	5	5		9			1	1		1			1	4		1	1			3		3		4	34	4.25
Toxorhamphus novaeguineae	11	7	14		10	1		4						2	5	5	5	1			4			Yes	9	60	5.45
Toxorhamphus poliopterus	5	8	4		8			1				1		1	4		1	2			2		5	Yes	5	34	6.8
Tregellasia leucops	4	6	3		6									1	3	2	3	2			3		1		3	27	6.75
Turdus poliocephalus	5				3																				12	15	3
Xanthotis polygrammus	5																							Yes	13	13	2.6

Bird Species	Number of samples	Number of invertebrate	Areneae	Chilopoda	Coleoptera	Dermaptera	Diplopoda	Diptera	Gastropoda	Neuroptera	Odonata	Orthoptera	Ricinulei	Hemiptera	Lepidoptera adult	Lepidoptera larvae	Hymenoptera: ants	Hymenoptera: others	Hymenoptera: bees	Hymenoptera: wasps	Insect:egg	Insect: larvae	Insect: pupae	Nectar	Fruit (+Seeds)	No. of invertebrates or fruits	No. of invertebrates or fruits in a sample
Zoothera heinei	4	3	1												1		1					1			1	5	1.25
Zosterops novaeguineae	4	5	1		3			1							1	2	1	1				1			1	12	3
Number of arthropods, fruits			397	17	711	21	9	137	15	24	16	40	10	141	101	261	200	248	6	13	189	23	138		766		
No. of bird species taking food			80	11	88	17	6	53	10	15	7	22	10	51	39	63	61	62	5	10	47	12	24		74		

Figure S1. Cluster analysis of species according to their diet based on identification into higher taxa listed in Table 3.

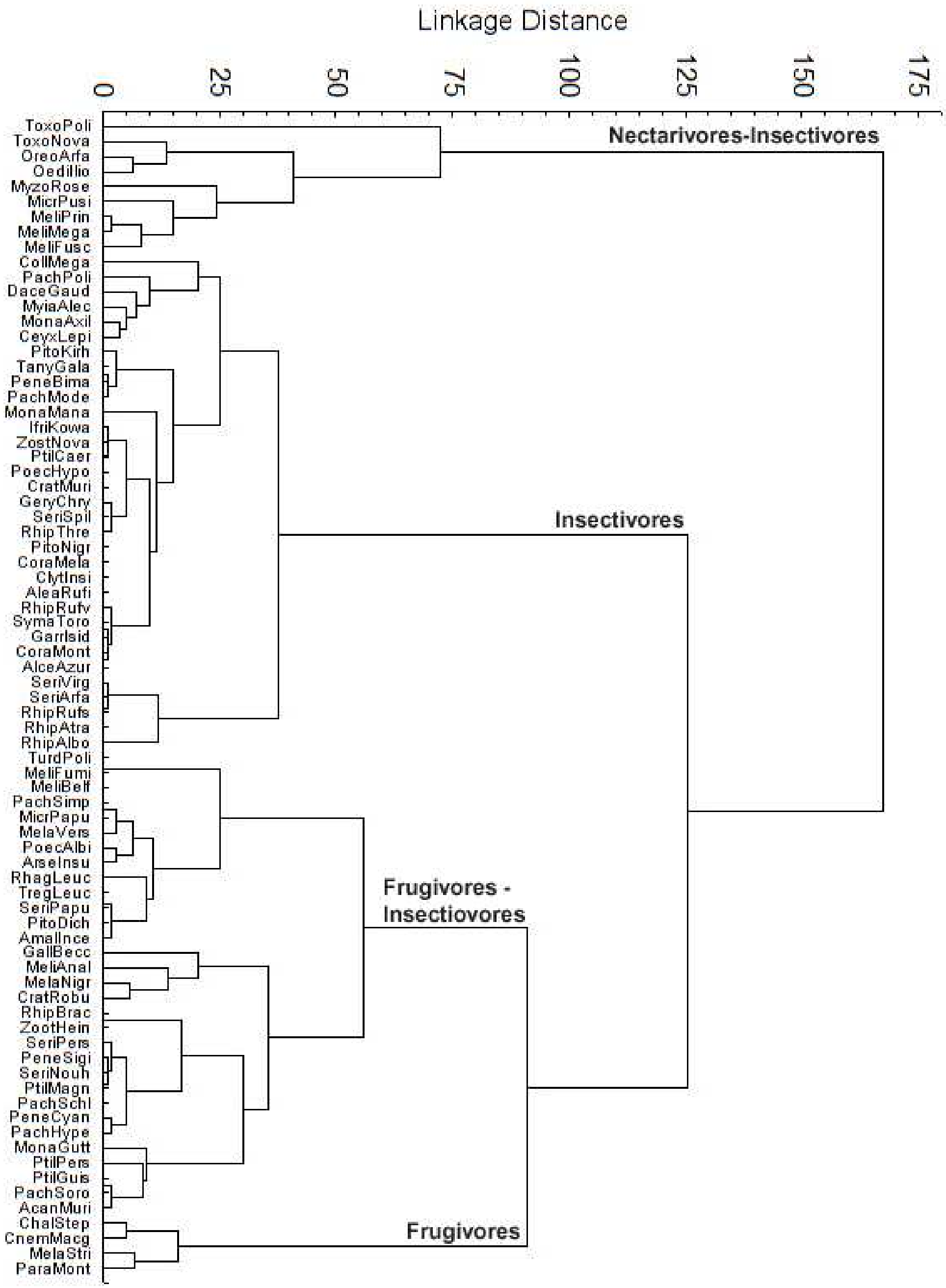


Figure S2. Cluster diagram of diet composition for four common bird species (*Colluricincla megarhyncha, Crateroscelis robusta, Melanocharis versteri and Sericornis perspicillatus*) sampled at the altitude 200, 700, 1200, 2200, 2700, 3200, and 3700 m asl. of Mt Wilhelm altitudinal gradient and at 1700 m asl. in Kotet (1700K). Diet identification is based on identification into higher taxa listed in Table 3.

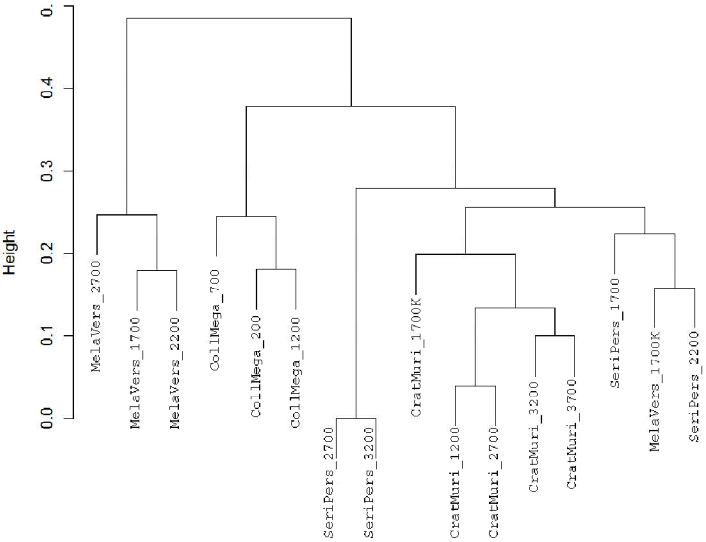
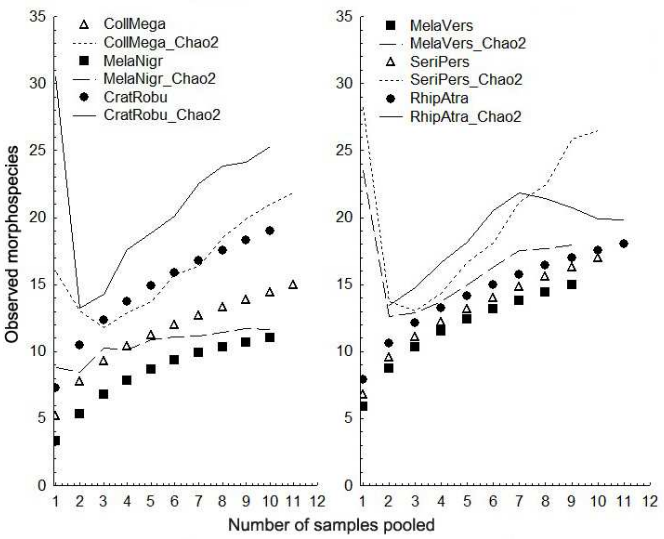


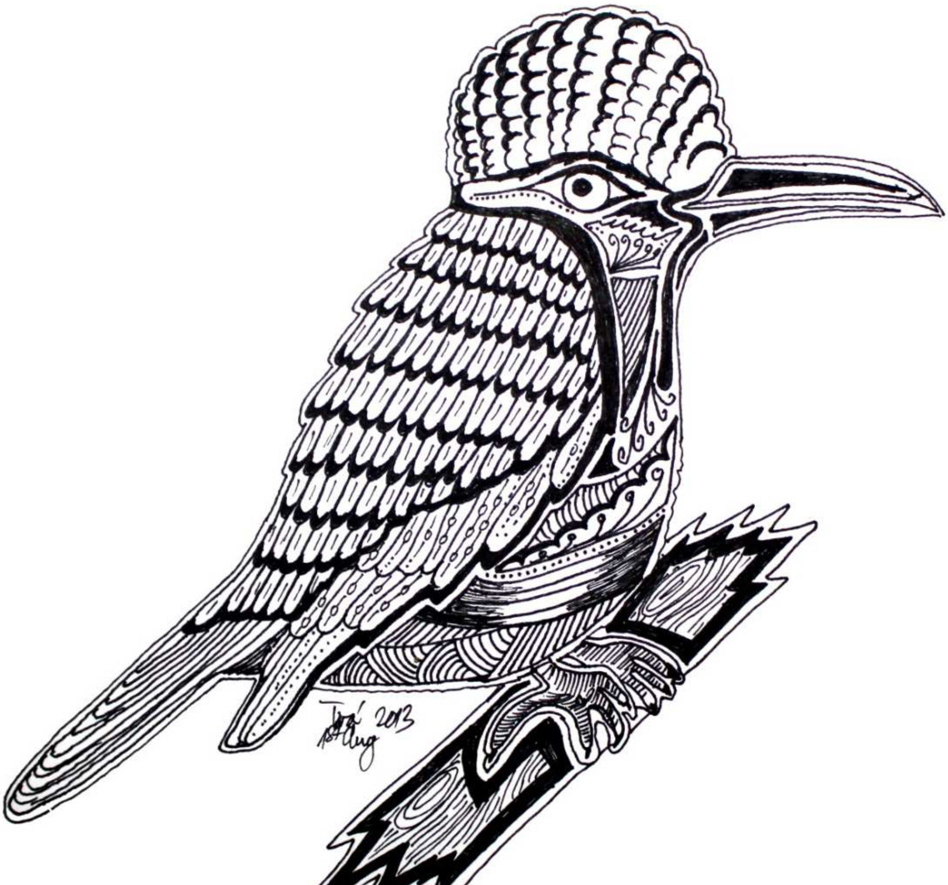
Figure S3. Randomised species accumulation curves for three selected species (with N ≥ 9 from the same altitude). Sample = regurgitated food from an individual bird. CollMega = *Colluricincla megarhyncha*, 200m; MelaNigr = *Melanocharis nigra*, 700m; CratRobu = *Crateroscelis robusta*, 2700m; MelaVers = *Melanocharis versteri*, 1700m; SeriPers = *Sericornis perspicillatus*, 2700m; RhipAtra = *Rhipidura atra*.



Chapter IV

Herbivore damage increases avian and ant predation of caterpillars along altitudinal forest gradient in Papua New Guinea

Katerina Tvardikova, Vojtech Novotny
(manuscript in review)



Herbivore damage increases avian and ant predation of caterpillars on trees along a complete altitudinal forest gradient in Papua New Guinea

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Abstract

Signals from plants to the predators that are attacked by herbivores may provide exciting examples of co-evolution among multiple trophic levels. We examined whether signals from damaged trees attract predators of insects along a complete altitudinal rainforest gradient in tropical region. We studied attacks by ants and birds, as the main predators of herbivorous insect, on artificial caterpillars. The predation rate decreased with altitude from 10% day^{-1} at 200 m asl to 1.8% day^{-1} at 3700 m asl. Constant predator-prey ratio and decreasing predation rate with altitude supports prediction of a higher incidence of anti-predatory defences, and aposematic signals in lowlands. Ants were relatively more important predators in the lowlands, while birds became dominant predators above 1700 m asl. Caterpillars exposed on trees with herbivorous damage were attacked significantly more than caterpillars exposed on trees without damage. The herbivory attracted both ants and birds, but its effect was stronger for ants.

Key Words: clay caterpillars, cry for help, Lepidoptera, predation, trophic interaction

Plants suffering from an attack by herbivores can actively reduce the number of herbivorous insects by attracting predators; this phenomenon, known as ‘‘plants crying for help’’, is due to a tritrophic interaction, in which the damaged plants are more attractive for natural enemies of herbivores. There is some evidence that plants have evolved to attract predators, but it is also possible to explain this as predators evolving to detect herbivores. Such a response has been documented for caterpillars and their parasitic wasps (De Moraes et al. 1998; Hoballah and Turlings 2001; Turlings et al. 1990). There are also reports on the increased attraction of predatory nematodes (Rasmann 2005), mites (Takabayashi and Dicke 1996; Vet and Dicke 1992), flies (Hulcr et al. 2005), true bugs (Mochizuki and Yano 2007) and thrips (Shimoda et al. 1997) to plants suffering from herbivory.

Recently, aviary behavioural experiments showed that birds could use visible feeding marks on plant leaves, or changes in reflectance as cues to find insect herbivores (Boege 2006; Heinrich and Collins 1983; Mäntylä et al. 2004; Mäntylä et al. 2007; Müller et al. 2006). Even if they could not see the herbivores or the defoliated plant parts, birds could discriminate herbivore-rich trees through olfactory detection of plant volatile compounds (Mäntylä et al. 2008). This is a relevant results since insectivorous birds are thought to be even more readily beneficial than insects to plants since avian predators can respond quickly and can considerably reduce herbivore load or damage to plants (Mooney et al. 2010; Van Bael et al. 2003; Van Bael et al. 2008).

Ants are recognized as another important predator of herbivorous insect in many ecosystems, tropical forests particularly (Hölldobler and Wilson 1990; Stamp and Bowers 1991). Their recruitment by damage-induced volatile compounds is known to increase rapidly following an attack by herbivorous insects on a host plant (Agrawal 1998; Fiala et al. 1989). These examples involved ants that had obligate relationships with their host plants and were thus more effective protectors than more common, opportunistic ants having facultative mutualistic relationships with plants (Heil and McKey 2003).

Both insectivorous birds and ants are important predators in most terrestrial communities, and the overall predation of caterpillars is determined to a large extent by their combined effects (Mooney 2007). Yet the strength of trophic cascades between plants, herbivores and ant or bird predators with ants or birds as predators can be quite variable both within (e.g. Mooney and Linhart 2006) and among communities (e.g. Shurin et al. 2002). The predation pressure experienced by a herbivore is thus a combined result of the local abundance of predators and their preferences for particular herbivores and/or their particular host plants (Barlow et al. 2006; Perfecto and Vandermeer 1996; Richards and Coley 2007; Richards and Phyllis D. C. 2008; Trollope et al. 2009; Zanette et al. 2000).

The altitudinal diversity and abundance gradient is one of the most striking biogeographic patterns on Earth (Rahbek 1995), and the role of multitrophic biotic interactions is a pervasive theme in efforts to understand these altitudinal gradients (Schemske et al. 2009). Altitudinal trends in predation pressure are poorly known in the tropics since most of the studies have focused on lowland forest (Novotny and Basset 2005), and relatively few studies have investigated biotic interactions along the entire altitudinal gradient (Schemske et al. 2009). Only few studies describe how predators, prey, and their interactions vary with altitude (Hodkinson 1999; Rodríguez-Castañeda 2012; Samson et al. 1997; Sivinski et al. 2000; Tvardikova and Novotny 2012).

Previously, we found that the frequency of bird attacks on artificial caterpillars increased from lowlands (200 m asl) to higher altitude (1700m asl, Tvardikova and Novotny 2012). To our knowledge, predation rate by ants or birds has not been studied along an comparable altitudinal gradient in the tropics. However, we expect decreasing predation rate in higher altitudes, as ants are generally thermophilic, and their diversity rapidly decreases with increasing distance from the equator and with increasing altitude (e.g. Dunn et al. 2007; Yusah et al. 2012). On the other hand, homoeothermic birds do not show such rapid decrease in diversity towards higher altitudes (McCain 2009). This means that they could become key predator at the higher altitudes, where ants are less abundant; however, we need replicated studies of predation rates across long or preferably complete altitudinal tropical gradients to test this hypothesis.

Direct studies of predation rates are scarce, particularly in comparison to the studies of herbivory or parasitism, because predation is momentary event that is particularly difficult to observe in tropical forests. Therefore, predation has also been documented by stomach content analysis, using both morphological and molecular methods of analysis (Symons and Beccaloni 1999). Alternately, predation pressure can be inferred from attack rates on baits, such as tuna baits for ant predation, or artificial caterpillars for bird predation (Howe et al. 2009; Posa et al. 2007).

Here we use artificial caterpillars exposed on plants across a complete tropical altitudinal gradient (200 – 3700 m asl) in Papua New Guinea to investigate predation pressure by two key predatory groups, ants and birds, and study their response to 1) simulated herbivory on tropical trees, 2) altitude , and 3) abundance of ants and birds in the studied forests.

Methods

Our study was performed along an altitudinal transect on the slopes of Mt. Wilhelm (4509 m asl) in the Central Range of the Papua New Guinea. The complete tropical altitudinal gradient spanned from the lowland floodplains of the Ramu River (200 m asl, S5 ° 44’ E145 ° 20’) to the timberline (3700 m asl, S5° 47’ E145° 03’). The transect comprised eight study sites, starting from 200 m asl and evenly spaced at 500 m altitudinal increments. The experiments were conducted in the wet season (April-June and September-October 2012) to eliminate possible changes in rainfall regime that can affect biotic interactions (Connahs et al. 2011; Preisser and Strong 2004; Stenseth et al. 2002).

Prior to the experiment, we selected 30 experimental trees from 2 - 3 locally common species at each altitude (listed in Table S1) which had at least 30 saplings 2.5 – 4 m high, which did not produce any exudate, did not have any ant nests, and were growing new leaves, largely without herbivore damage. We used either 10 saplings from each of three species, or 15 saplings from two species at each altitude. We tried to find trees with low herbivory damage on old leaves, and avoided trees with damage on young trees.

We used artificial caterpillars exposed on the study trees to monitor attacks by natural enemies. Caterpillars were made from natural-looking dark green colour modelling clay (Koh-I-Noor Hardtmuth brand), which is malleable, oil-based and non-toxic. We modelled artificial caterpillars by pressing the plasticine through a syringe to ensure that each caterpillar had an absolutely smooth surface. Artificial caterpillars were 15 mm long and 3 mm in diameter, matching in body size locally common crambid and tortricid caterpillars, and also matching the median caterpillar size in the entire caterpillar community (Novotny and Basset 1999), as well as the size of caterpillar most commonly taken by birds (Tvardikova, unpubl. data). This method has been successfully used in previous study (Tvardikova and Novotny 2012).

Each experiment was conducted along a single 2250 m long transect at each study site. Thirty sampling points, represented by individual trees, were spaced at approximately 75 m intervals along transect. This spacing ensured that the experimental trees could be considered independent, as the phenomenon of transmission of volatile compounds between two plants requires air contact, and was detectable up to 60 cm in the field conditions (Karban 2007). Ten artificial caterpillars were placed on each tree, between 2.5 and 4 m above the ground. Artificial caterpillars were pinned on the distal half of young leaves such that the head of pin was hidden in modelling clay. Actual caterpillars present on sapling were removed from the trees prior to experiment so they did not bias the herbivore density. A subset of leaves on every second experimental tree were cut by scissors so that 5 % of original leaf area was damaged and removed, simulating herbivory. The damage by scissors was repeated daily (resulting in 5% of leaf area removed every 24 hours from each tree) to ensure that potential attraction of leaf damage to predators remained constant for the duration of experiment. The overall experimental damage to leaves was thus increasing from 5 to 25 % of leaf area in the course of the experiment. Previous studies showed that only fresh leaf damage attracted ants (Karban 2007). Leaves for experimental herbivory were randomly selected from the entire sapling.

We exposed 10 artificial caterpillars per tree, i.e. a total of 300 caterpillars along the transect at each study site, including 150 placed on trees with artificial herbivory damage and 150 on undamaged trees. Each caterpillar was inspected at 24-h intervals for five consecutive days and carefully examined for characteristic bite marks or signs of parasitism (Tvardikova and Novotny 2012). Caterpillars attacked by two different predators (N = 23) in same day were treated as two independently attacked caterpillars. Missing caterpillars were excluded from the analyses as their status could not be ascertained. All missing caterpillars and caterpillars with marks of attack were replaced by new ones, pinned to approximately the same locations (Koh and Menge 2006; Posa et al. 2007; Tvardikova and Novotny 2012).

Bird sampling

We surveyed bird communities by two types of census at each altitude – point counts and mist-netting. Point counts were carried out at 16 points regularly spaced along the 2175 m long transect. We conducted five point-count surveys during the duration of experiment with caterpillars. Further, we mist-netted birds (under license CZ-1062) into a 200 m long line of nets for 3 days (using nets 2.5 m high x 12 - 18 m long, mesh 16 mm) from 5:30 am to 5:30 pm daily, with regular checks every 20 minutes. We classified all recoded species into feeding guilds and strategies, and used the number of insectivorous species occurring in understory and mid-story at each altitude for the analysis.

Ant sampling

We surveyed ant communities occurring on experimental trees by observation and hand collection, as well as using tuna baits. Observation of ant activity was performed prior to the exposure of caterpillars. The trunk of each tree was examined for 10 minutes, all foraging ant individuals were counted and voucher specimens were taken for identification. Commercial canned tuna was used in baits, which is a standard method in the studies of foraging ant communities (Janda and Konečná 2011). One tea spoon of tuna was placed as bait under a stripe of gauze at breast height at each experimental tree. Baits were inspected one and three hours following their exposure. All ants present were counted and voucher specimens for each species were collected without disturbing the remaining ants. We used combination of two methods, to eliminate for known fact, that not all ant species are attracted to bait (e.g. Véle et al 2009).

Statistical analyses

The data across five experimental days (from 1 to 5) were clumped together, because daily number of attack was low and did not differ between days (H_4 = 7.05, P = 0.13 – n = 150 - H_4 = 9.26, P = 0.06, n = 150). Prior to analyses, we excluded all unidentified attack attempts (1 %) and lost caterpillars (2 %) from the analysis. The effect of altitude and herbivory on the incidence of attacks was tested by ANOVA with nested design and two within-category effects. All 30 sampling trees were nested in each of the eight experimental sites. Percentages of caterpillars attacked at each sampling tree were arcsine transformed to meet conditions of normality. Presence or absence of herbivory was used as the first within-sampling effect and the type of predator (birds, ants, wasps or other insect) as the second within-sampling effect. Tukey post hoc tests were performed to inspect differences between altitudinal sites and predator taxa.

Further, numbers of caterpillars attacked by various predators were regressed against the abundances of predators or their species richness. All analyzes were conducted in Statistica 9 (StatSoft, Inc. 2010).

Results

We exposed a total of 2,400 caterpillars for five days, resulting in 12,000 caterpillar-days of exposure, during which we identified 1,790 attack attempts. Median number of attack attempts for trees with herbivory was 5 and 3 on trees without herbivory across the whole gradient. Mean predation along the whole gradient was 10 ± SE 0.8% d^{-1}.

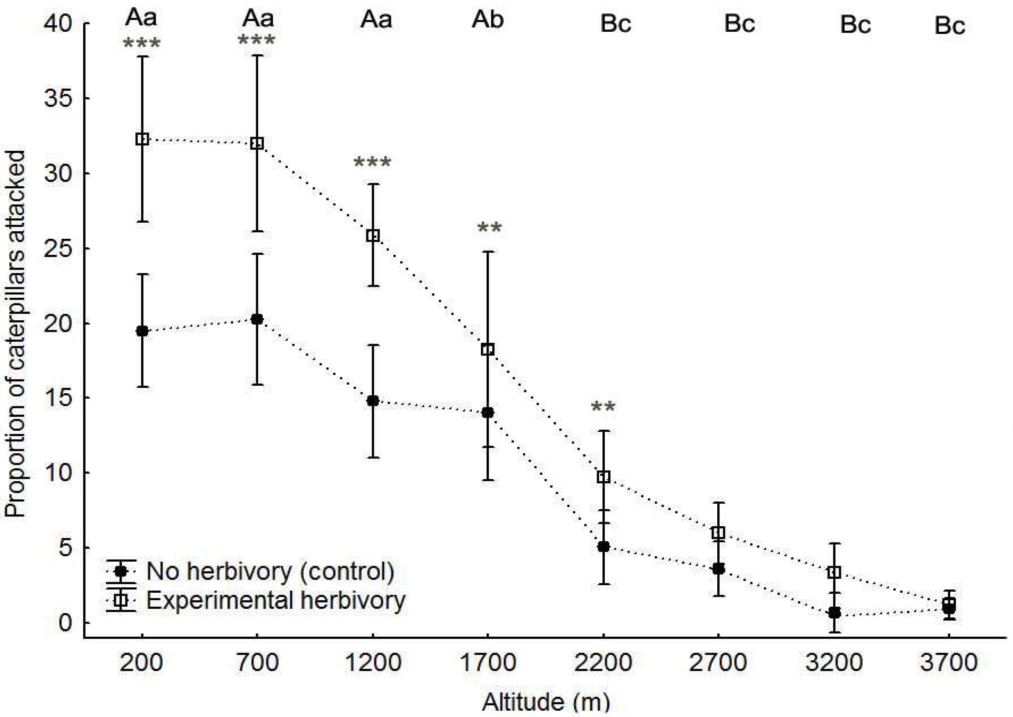

Figure 1. Mean percentage of caterpillar attacks by all predators during 5 days of exposition on one tree with (N = 75) or without (N = 75) simulated herbivory at each altitudinal site. Sites with significantly different rates of attacks between trees with and without herbivory are marked by asterisks (*** $P < 0.001$, ** $P < 0.05$; Tukey post-hoc test). Altitudes with significantly different incidence of attack ($P < 0.05$) are

denoted by different letters; capital letters = trees with herbivory, small letters = trees without herbivory (Tukey post-hoc test).

Table 1. Effects of altitude (8 sites, 200 - 3700 m asl, 500m altitudinal increment), and herbivory (present or absent), and predator (bird, ant, wasp, other insect) on the incidences of attack on caterpillars. Repeated-measures ANOVA with two within effects.

	SS	df	MS	F	P
Altitude	5.06	7	0.72	100.36	<0.001
Herbivory	0.41	1	0.41	61.11	<0.001
Herbivory * Altitude	0.11	7	0.01	1.39	0.085
Predator	5.45	3	1.81	284.55	<0.001
Predator * Altitude	3.58	21	0.17	26.68	<0.001
Herbivory * Predator	0.06	3	0.02	3.87	0.009
Herbivory * Predator * Altitude	0.28	21	0.01	2.32	<0.001

The percentage of attacked caterpillars was significantly higher (effect of altitude, Table 1) in the lowland forests (14.3 ± 5.4% d^{-1} of all attacks at 200 m asl and 16.6 ± 4.3% d^{-1} at 700 m asl), and decreased with altitude towards 1.8 ± 1.1% d^{-1} at 3700 m asl. This pattern was observed for both trees with and without herbivory (Fig. 1). In total, trees damaged by herbivory (11.4 ± SE 1.2% d^{-1}) had significantly (effect of herbivory, Table 1) more attacked caterpillars than trees without herbivory (8.9 ± SE 1.3% d^{-1}; Fig. 1). This pattern did not change across the gradient (interaction herbivory and altitude, Table 1). However, the attacks on trees with herbivory was significantly higher on trees without herbivory at only the five lower altitudes (200, 700, 1200, 2200 m asl; Fig. 1), but not at the higher altitudes.

The majority of all recorded attacks on caterpillars were made by birds (52 %), and ants (38 % of recorded attacks). Attacks of birds and ants showed significant results (Fig. 2), and drove observed patterns. The attacks by other predators (wasps = 4%, all other insect = 6 %) were low. Neither altitude (Tukey post-hoc test results for other insect: P > 0.304, wasps: P > 0.06) nor herbivory (other insect: P > 0.51, wasp: P > 0.08) had significant effect on the number of their attacks. Both ants and birds attacked caterpillars exposed on trees with artificial herbivory damage significantly more than caterpillars exposed on trees without damage (results of Tukey post-hoc tests for birds and ants; Fig. 2). Attractiveness of trees with herbivory damage across all altitudes was higher for ants than for birds (ANOVA; ants: SS = 175.98, F = 12.027, P < 0.001; birds: SS = 32.46, F = 7.31, P = 0.007; Fig. 2).

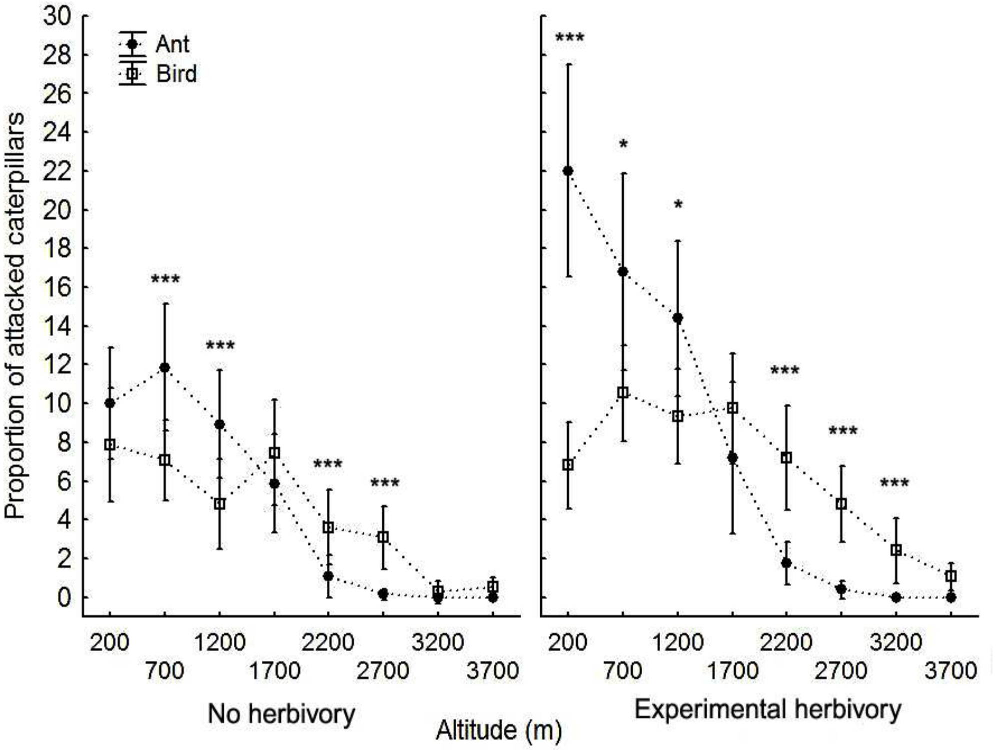

Figure 2. Mean percentage of caterpillar attacks by ants and birds recorded during 5 days of exposition on one tree with (N = 75) or without (N = 75) simulated herbivory. Sites with significantly different rates of attacks by ants and birds are marked by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). Differences in the attack rates on caterpillars between trees with and without herbivory for birds: P = 0.43 – 200m, 0.01 – 700m, 0.03 – 1200m, 0.1 – 1700m, 0.001 – 2200m, 0.15 – 2700m, 0.23 – 3200m, 0.78 – 3700m, and ants: 0.008 – 200m, 0.008 – 700m, 0.01 – 1200m, 0.2 – 1700m, 0.02 – 2200m, 0.15 – 2700m, no variance – 3200m, no variance – 3700m. Results of Tukey post-hoc test from repeated measures ANOVA are presented.

Birds attacked the highest number of caterpillars (in both experimental settings summed, and experiment setting) at 700 m asl. The predation rate of birds correlated with the number of insectivorous bird species ($R^2 = 0.82$, $F_{1,6} = 28.62$, $P = 0.002$, $n = 8$) and abundances of insectivorous birds ($R^2 = 0.78$, $F_{1,6} = 21.36$, $P = 0.003$, $n = 8$) recorded (Fig. S2). The number of attacks on caterpillars exposed on leaves with herbivory correlated significantly with the number of bird species ($R^2 = 0.80$, $F_{1,6} = 24.39$, $P = 0.002$, $n = 8$) and bird individuals recorded at each site ($R^2 = 0.78$, $F_{1,6} = 21.63$, $P = 0.003$, $n = 8$; Fig. 3). Number of attacks on caterpillars on control trees correlated with the number of bird species ($R^2 = 0.63$, $F_{1,6} = 10.14$, $P = 0.01$, $n = 8$) but not with the number of bird individuals ($R^2 = 0.47$ $F_{1,6} = 5.41$, $P = 0.06$, $n = 8$). Birds attacked relatively more caterpillars than ants only at altitudes above 1700 m asl (Fig.

2). From our test treating the missing and fallen caterpillars as predated on by birds also did not influence the results significantly ($F_{1,23998}$ = 0.56, P = 0.45).

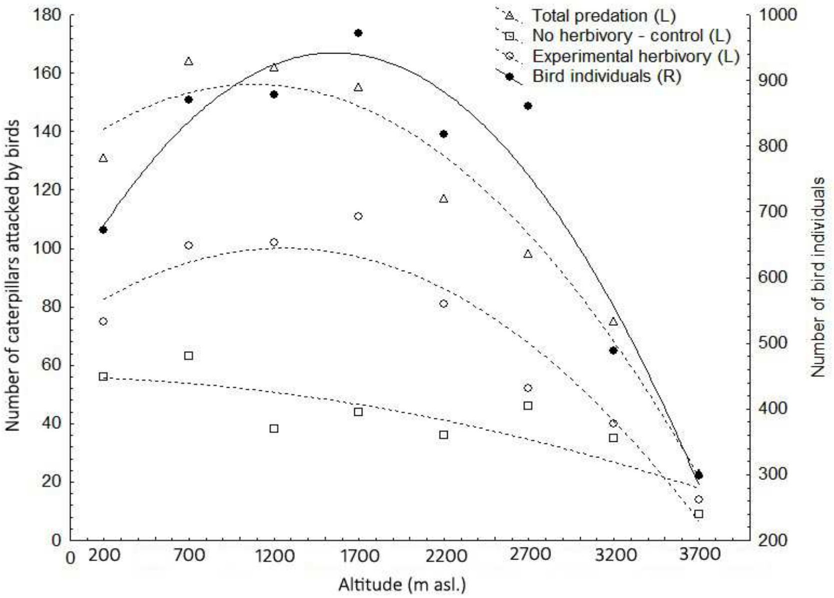

Figure 3. Number of caterpillars attacked by birds during the whole experiment correlated with number of bird individuals present at site. Total predation by birds = 133.2721+0.0423*x-1.9595E-5*x^2, on Control trees = 56.0379-0.0016*x-2.3571E-6*x^2, and on Experimental herbivory trees = 75.3329+0.0394*x-1.5667E-5*x^2, Individuals of insectivorous birds observed = 596.5814+0.4444*x-0.0001*x^2

Ants attacked the largest number of caterpillars at lower altitudes whilst only 4 caterpillars (0.3%) were attacked by ants at 2700 m asl during whole experiment. No ant attacks were observed at 3200 and 3700 m asl. The number of caterpillars attacked by ants correlated significantly with number of trees infested by ants at each altitude (direct observations R^2 = 0.91, $F_{1,6}$ = 64.95, P < 0.001, n = 8; exposition of tuna baits for three hours R^2 = 0.94, $F_{1,6}$ = 113.68, P < 0.001, n = 8; Fig. 4).

The correlation of caterpillar attacks with the number of ant individuals sampled from those trees (observed or present on tuna baits) was also significant but explained a lower proportion of variability in caterpillar attacks (observations R^2 = 0.63, $F_{1,6}$ = 10.34, P = 0.038, n = 8; tuna baits R^2 = 0.80, $F_{1,6}$ = 25.37, P = 0.002, n = 8; Fig. 4). Ant abundance decreased with altitude from 200 to 2700m asl (tuna baits: Number of trees with ants = -0.0077*altitude + 22.436, n = 8; R^2 = 0.97; Number of individuals = -954.3ln(altitude) + 1584.5, R^2 = 0.91; n = 8).

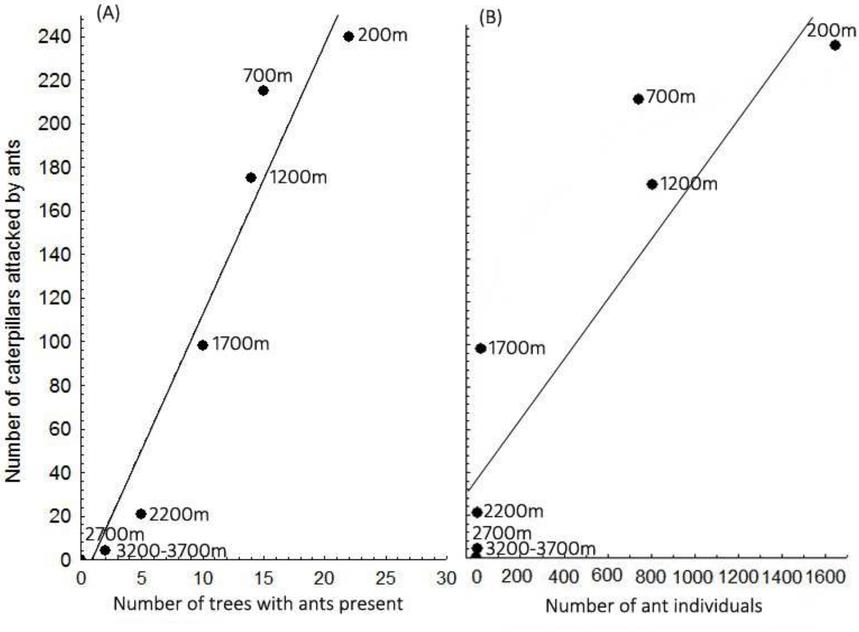

Figure 4. The number of trees with ants present influences significantly the number of caterpillars attacked by ants during whole experiment (A). The abundance of ants on experimental trees measured at tuna baits on trees with and without experimental herbivory together did influence the number of attacks less significantly (B).

Discussion

Our results demonstrate the importance of leaf damage as a herbivore presence cue, ants and birds, the two most important groups of predators in tropical forests. The effect of herbivory is probably important along the entire altitudinal gradient, although the number of attacks observed above 2200 m asl was too low for rigorous tests. We reported approximately two times higher daily predation on trees with damaged leaves than on control leaves, which corresponds to other studies reporting on the effect of herbivory on predation or attractiveness of predators to herbivore infested plant (Kessler and Baldwin 2001). Two times higher daily predation rate results in five times higher mortality in five days, which makes caterpillars present on trees with herbivory much more susceptible to predation during their life-time. The trend is significant both for ants and birds at many altitudes, but the response to herbivore is particularly strong by ants.

The phenomenon of induced attraction of carnivorous arthropods by plants in response to herbivory is now well accepted (Takabayashi and Dicke 1996). Leaf damage may be a stronger inducer of ant activity than sole presence of herbivore (Agrawal 1998): study reports as much as a fivefold increase in ants on damaged leaves 12 minutes after herbivorous damage, and twofold increase in ants on damaged leaves after 24 hours, compare to simple undamaged control leaves. Similarly, Romero (2004) reported three times more ants on young leaves with damage compare to undamaged leaves.

Decreasing predation rate with altitude leads to the prediction of a higher incidence of anti-predatory defences, such as chemical or behavioural, in the lowlands, particularly against ants (Agrawal and Rutter 1998; Schmidt 1990). Further, the frequency of aposematic signals is expected to decrease with altitude. The linear relationship between the abundance of predators and the attack rate on caterpillars suggests that predator/prey ratio remains approximately constant along the altitudinal gradient. Further, it implies that the efficiency of predators in finding their prey does not change with altitude, despite the decrease in vegetation complexity with altitude (Tvardikova, unpubl. data). Šipoš and Kindlmann (2012) conclude that even with a constant predator-to-prey ratio, increasing vegetation complexity may lower attack rate on prey. This was not the case in our study, possibly because it was limited to the understory of primary forest.

The results of experiments with artificial caterpillars have to be interpreted with caution, as clay caterpillars provide only visual cues to their natural enemies; hence it does not test for predators react to defensive or deterrent behaviours (Gentry and Dyer 2002). Further, insect feeding on plants under natural conditions leaves other traces that could reveal them to natural enemies (Gentry and Dyer 2002; Murakami 1999; Vet and Dicke 1992; Weiss et al. 2004). Such clues could be very different for individual natural enemies and, and likely different enemy taxa handle live insect prey in different ways (Dyer 1997; Dyer 2002; Hölldobler and Wilson 1990). The method used could therefore lead to the exclusion of important specialist predators.

The design is undoubtedly biased towards generalist predators that queue out on visual and mechanical plant damage. However, the incidence of attack on our artificial caterpillars (exposed on leaves with and without herbivory) per 24 hours was similar to incidence of attack measured on genuine exposed caterpillars in exclosure experiments (7.5% ± 6.7%, median = 5.8%, nine studies from both tropical and temperate habitats (Remmel et al. 2011); and consistent with the results from our previous study which used the same artificial caterpillars (Tvardikova and Novotny 2012). Manipulative studies using artificial caterpillars recorded similar daily attack rates of 11.1% (Richards and Coley 2007) in a lowland seasonal forest in Panama, 13.7% in semi evergreen lowland dipterocarp forest in the Philippines (Posa et al. 2007), and 5.8% - 52.4% in three studies from various tropical areas (Remmel et al. 2011).

Experimental damage on leaves in our study attracted ants, which are chemically oriented predators, as well as mainly visually oriented birds. We used mechanical damage to simulate herbivory on foliage and this may be a less efficient cue to predators than the damage done by herbivores feeding, therefore underestimating the significant effect of predators observed in this study. From the literature it is unclear for how long would a tree with high leaf damage remain attractive to predators. Bolter (1997) reported that wounds healed rapidly after cutting, and their attractiveness to herbivores disappeared shortly after cutting the leaves. In other experiments, emissions of compounds that attracted predators and parasitoids waned within minutes after mechanical clipping, but remained 1 – 3 days after actual chewing damage or application of insect regurgitant (Steinberg et al. 1993; Turlings et al. 1995). In contrast, Karban (2007) reported that mechanically clipped shoots attracted predators for up to 6 days following clipping. In order to compensate for lower efficiency of mechanical damage, we decided to repeat it daily during our experiments. We expected that response to damage is systemic, and undamaged leaves of injured plants also emit terpenoids based signals (Turlings and Tumlinson 1992). Future studies of how ants respond to volatile compounds released by damaged plants across elevation are needed to understand what influences predation by ants across altitude.

It is worth noting that a daily mortality rate of 1%, 5% and 20% over the 3-weeks caterpillar lifespan would produce overall mortality of respectively 19%, 66% and 99%. We assume that the predation rate observed in this study is plausible since it corresponds to what is available from the literature in both temperate 78% in Kentucky (Choate and Rieske 2005) and tropics 68% in Campinas, Sao Paulo (Gomes-Filho 2003). Further, even if our experiments using models of caterpillars did not provide an estimate of natural predation rates, the relative number of predation incidents should be comparable among habitats (Brodie 1993) for individual species of generalist predators.

Schwenk et al. (2010) did not find any effect of altitude on bird predation of arthropods between 290 and 780 m asl, while we found higher predation rate at 1700 m than at 200 m asl (Tvardikova and Novotny 2012). This was consistent with the pattern observed in the present study, where the highest predation by birds was in mid-altitudes (700 – 1700 m asl). The higher abundances of insectivorous birds in mid-altitudes, and the relatively gradual decrease of their abundances have been observed in many other studies (McCain 2009). These suggest that birds drive the predation rates of caterpillars at altitudes, where ants are relatively rare (i.e. 1700 m asl; Fig. 2). Thus, relative importance of predation of ants is more important towards the lowland forests

(200 – 1700 m asl) and it decreases with altitude; whereas bird predation become more important at mid-altitudes (1700 – 2700 m asl).

We observed a dramatic drop in abundance of ants at high altitudes which correlated with the predation rate observed. This result substantiated previous studies which observed markedly reduced species richness and abundance of ants at higher altitudes (Bito et al. 2011; Bruehl et al. 1999; Samson et al. 1997; Yusah et al. 2012), most likely resulting in a decrease in predation pressure on herbivorous insect. The number of trees and baits occupied by ants proved to be better correlated with predation rates than the total abundance of ants in the samples. It appeared that abundance of ant individuals influences only the number of bites into one caterpillar, and not the number of predated caterpillars.

In conclusion, our study demonstrates (i) the large importance of plant damage as a cue of herbivore presence for predators (particularly true for ants but also observed in birds) (ii) decreasing attack rate of predators with increasing altitudes in tropical forests, and (iii) a transition in predator dominance from ants in the lowland forests to birds at the mid to high altitudes. Further, the change in dominant predator group with altitude could lead to dramatic changes in anti-predation strategies of herbivores, and the structure of local food webs, along altitudinal gradient.

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SUPPLEMENTARY MATERIAL

Table S1. Tree species used in experiments at each altitudinal site

Figure S1. The number of bird species (A) and individuals (B) per study site had significant effect on the number of caterpillars on trees with experimental herbivory attacked by birds.

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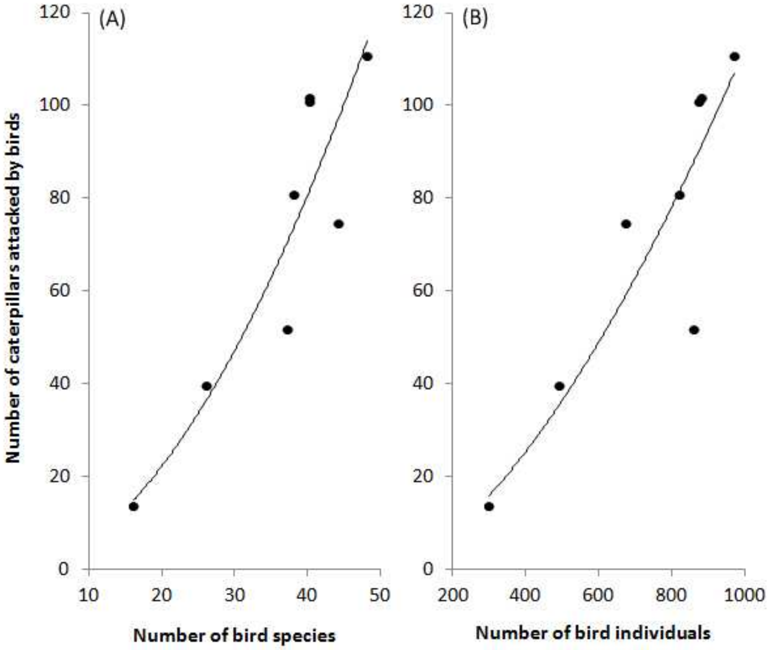
SUPPLEMENTARY MATERIAL

Table S1. Tree species used in experiments at each altitudinal site

Tree species/Altitude m	200	700	1200	1700	2200	2700	3200	3700
Aglaia lepiorrhachis		X						
Chionanthus ramiflora		X	X	X				
Cryptocarya multipaniculata				X				
Dillenia papuana					X			
Ficus wassa	X							
Gnetum gnemon	X							
Nothofagus grandis					X			
Pittosporum ferruginea							X	
Platea excelsa					X			
Podocarpus sp.						X	X	X
Quintinia sp.						X	X	X
Sterculia schumanniana	X	X	X	X				

Figure S1. The number of bird species (A) and individuals (B) per study site had significant effect on the number of caterpillars on trees with experimental herbivory attacked by birds. Number of species: R^2 = 0.88, $F_{1,6}$ = 24.39, $P < 0.002$, Number of attacks = 0.0015*Number of species^1.6229; Number of individuals: R^2 = 0.92, $F_{1,6}$ = 21.79, $P < 0.003$, Individuals = 0.0858*Number of individuals^1.8573



Chapter V

Disappearance of birds from forest fragments in Papua New Guinea

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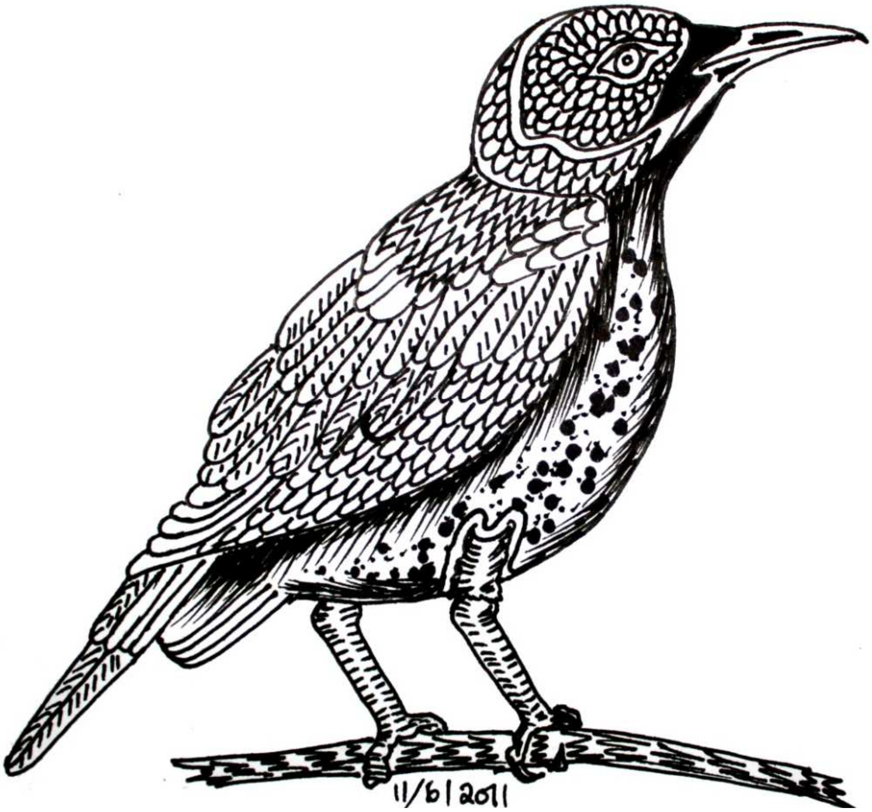
(manuscript in review)



Disappearance of birds from forest fragments in Papua New Guinea

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Abstract

Tropical forests worldwide are being fragmented at a rapid rate, causing a tremendous loss of biodiversity. Determining the impacts of forest disturbance and fragmentation on tropical biotas is therefore a central goal of conservation biology. Here we focus on bird communities in forest fragments (300, 600 and 1,200 ha) in the lowlands of Papua New Guinea and compare them with bird communities in continuous forest. Size of forest fragments did not prove to have a significant effect on the number of locally recorded birds, and we recorded 80, 82 and 84 forest bird species in fragments and 107 in continuous forest. We show that large bodied frugivores and understory insectivores are particularly sensitive to habitat fragmentation. We did not find strong support for the food scarcity hypothesis which states that the decline of insectivorous birds in forest fragments is caused by an impoverished invertebrate prey base. Neither have we found significant difference in microclimate in forest interiors. Rather, we show that the microhabitats preferred by sensitive birds were scarce in forest fragments, but common in continuous forest. Our results thus support the hypothesis that changes in microhabitats make forest fragments unsuitable for certain, sensitive species. Although none of the studied forest fragments was large enough to sustain complete bird communities found in primary forest, they housed large numbers of bird species, and they are easily protected on village basis in the conditions of Papua New Guinea.

Keywords

food limitation, habitat selection, insectivorous birds, forest fragmentation, frugivorous birds, microhabitat, tropical forest, rainforest conservation, species loss, local extinction

Lowland forests of the wet tropics support the most species rich communities of terrestrial birds. Unfortunately, they are under intense threat of disturbance by selective logging and conversion to plantations (Barlow et al., 2006), which leads to fragmentation of the initially continuous forest cover found in many tropical areas. Unfortunately, forest fragmentation almost always leads to local loss of species (Turner, 1996). Recent research has focused mainly on Neotropical forest conversion (Komar, 2006) and fragmentation (Sekercioglu et al., 2002). More information on the impacts of this process from other tropical forest systems is needed, particularly from Africa (Newmark, 1991) and Pacific Ocean islands (Marsden et al., 2006), where the deforestation is intensifying (Shearman et al., 2008).

Our previous work in primary and secondary forest in Papua New Guinea (Tvardikova, 2010) demonstrated high sensitivity of lowland insectivorous birds and canopy frugivores to forest disturbance. Other authors have also reported large frugivorous and terrestrial and understory insectivorous birds to be sensitive to habitat change (Stouffer and Bierregaard, 1995, Sekercioglu, 2002, Sekercioglu et al., 2002, Kattan et al., 2004, Lees and Peres, 2010). Insectivores have generally low mobility and are more confined to forest interior than other forest passerine guilds. They are usually more specialized in their foraging techniques and use narrower habitats and microhabitats (Terborgh et al., 1990, Stouffer and Bierregaard, 1995). Insectivores seem to be more sensitive to subtle habitat changes because, unlike fruits, flowers, and seeds, invertebrates actively avoid insectivores and, as a result, insectivorous birds have evolved into many specialized niches and seek prey in certain microhabitats.

Over a dozen of hypotheses have been proposed to explain the disappearance of insectivorous bird species from forested habitats around the world (Canaday, 1996, Ford et al., 2001). Four of these are particularly relevant to the decline of understory insectivores: The food scarcity hypothesis states that small fragments are impoverished in prey preferred by understory insectivores (Ford et al., 2001, Burke and Nol, 1998, Zanette et al., 2000). The microclimate hypothesis proposes that these birds are particularly sensitive physiologically to changes in microclimate associated with forest fragmentation (Karr and Freemark, 1983, Canaday, 1996). The habitat specificity hypothesis states that the loss of some microhabitat elements (such as army ant swarms, dead trees) from fragments may affect many understory insectivores (Canaday, 1996, Ford et al., 2001). Finally, according to the limited dispersal hypothesis, understory insectivores, because of their relatively sedentary habits and possible behavioural avoidance of clearings and altered habitats (Stouffer and Bierregaard, 1995, Báldi, 1996, Sekercioglu, 2002), may be less likely to disperse into more favourable habitats after forest fragmentation and may disappear from fragments as a result of stochastic events.

Our objective was to quantitatively describe bird communities and their response to forest fragmentation in lowland tropical forest in Papua New Guinea and test the above hypotheses on the causes of species loss. Papua New Guinea forests are continuous over large areas and they represent one of the last three tropical wilderness areas along with Amazonian and Congo forest (Mittermeier et al., 1998). However, they are presently under increasing threat from logging (Shearman et al. 2008). The response by birds to forest fragmentation in Papua New Guinea has received little attention. We focused on birds in a continuous forest (>10,000 ha) and forest fragments of different sizes (300, 600 and 1,200 ha), in order to identify the size of forest fragments which would be sufficient to maintain local species richness and functions similar to continuous forest, and to determine which of the four proposed hypotheses might explain declines in understory insectivores.

Methods

Research Sites Field work was conducted in June 2010, October 2010 and January 2011 in primary forest and forest fragments in the lowlands of Madang province, Papua New Guinea (PNG). The study sites were (1.) continuous forest (5° 13.5' S, 145° 04.9' E, 120 m a.s.l.) situated in the middle of >10,000 ha of continuous lowland primary forest in Wanang Conservation Area, which itself is embedded within ~100,000 ha of selectively logged, but largely contiguous lowland rainforest; (2.) a large fragment (5° 01.73' S, 145° 46.01' E, 100 m a.s.l.) – 1200 ha fragment of forest near villages Rempi and Baiteta; (3.) a mid-sized fragment (5° 07.99' S, 145° 45.47' E, 100 m a.s.l.) - 600 ha forest fragment near village Baitabag, (4.) a small fragment (5°16.2' S, 145°41.1' E, 170 m a.s.l.) - 300 ha fragment of lowland primary forest near Ohu village. All fragments are located in relatively densely settled and intensely farmed landscape around Madang town, 15 – 24 km from each other, and 67- 76 km from the site in continuous forest (Fig. 1). The fragments have been increasingly isolated since the 1980s as the original mosaic of primary and secondary forests around villages changed into a more intensely managed landscape with slash-and-burn food gardens, young secondary forest growing on abandoned gardens, deforested village settlements, and plantations. All fragments have been preserved as village-based protected areas, where logging and hunting is forbidden. The village landowners supervise the forest preservation. Likewise, the continuous forest has been declared by village landowners as a conservation area with no logging and hunting (www.entu.cas.cz/png/wanang).

The location and size of the studied forest fragments is representative of other landscapes in Madang province and lowland PNG at large, where most of the inland area is still covered by continuous forest (although under increasing logging pressure) whilst large areas along the coast are now a mosaic of food gardens, villages, secondary and selectively logged forests, and plantations. A few villages where landowners have interest in conservation protect fragments of primary, undisturbed forests, similar to the ones in which we conducted our research.

All study sites have a humid climate with a mild dry season from July to September; the average annual rainfall is 3600 mm (McAlpine et al., 1983). Humidity, temperature and dew point were recorded every 30 min for the duration of experiments (15 days) using data loggers (Comet R3120) placed in the forest interior at each fragment (of study site in continuous forest). All study forests had a closed, approximately 35 m high canopy and relatively open understory without distinct stratification.

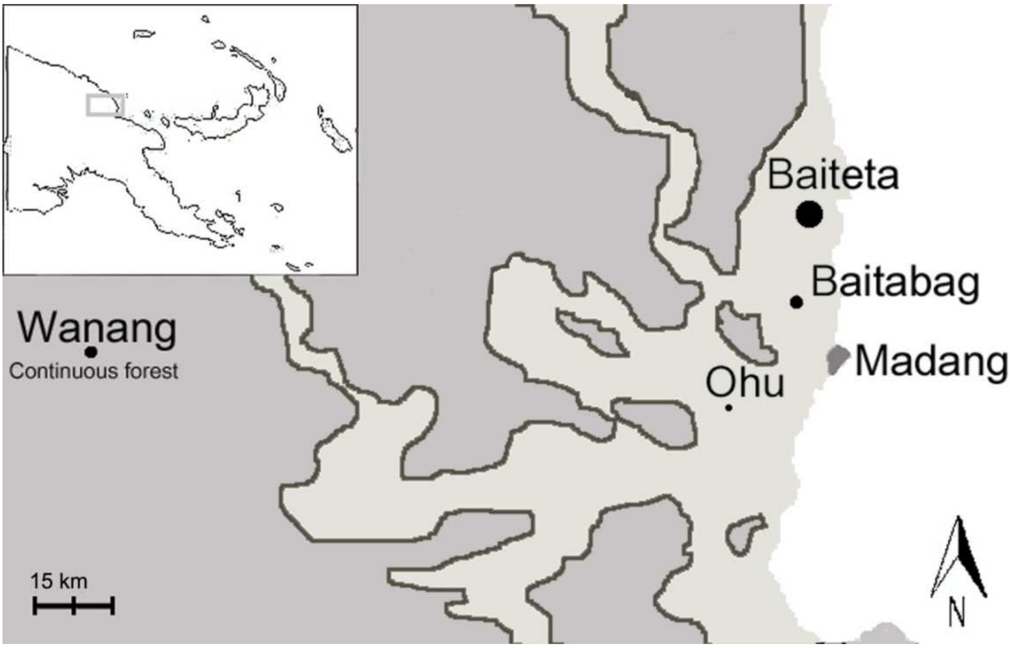

Figure 1. Location of study sites in Papua New Guinea (inserted map) and in the Madang Province. Baiteta = forest fragment 1200 ha, Baitabag = forest fragment 600 ha, Ohu = forest fragment 300 ha, Wanang = continuous forest area > 10,000 ha. Dark grey = undisturbed forest, light grey = (selectively) logged or altered forest and plantation.

Bird surveys Bird communities were surveyed by three types of census – point counts, mist-netting and random walks. Point counts were carried out at 16 points regularly spaced along a 2250 m transect (successive points were 150 ± 5 m apart to avoid overlap). All birds seen or heard were recorded in the following radial distance classes in meters: 0 - 10, 11 - 20, 22 – 30, 31 – 40, and 41 – 50. We started censuses 15 min before day break, at a randomly selected point. Each counts lasted 15 minutes so that all 16 points were surveyed before 11:00. We conducted nine replications at all points, resulting into 36 hr of observation at each site. All point-counts represented heterogeneity of lowland forest habitats in similar way (i.e. survey points included hill ridges, creeks, natural canopy openings, etc.). Further, we mist-netted birds into 200 m long line of nets for 6 days (using nets 2.5 m high x 12-18 m long, mesh 16 mm), from 05:30 to 17:30, with checks every 20 min. We identified all mist-netted individuals into species, marked them individually by colour rings, and released within 10 min. Finally, we walked along the tracks and throughout the area and constructed continuous list of species during the random walks. Walks lasted 2 – 3 hr day-1 (starting at 15:00), and were standardized to 20 hr site-1. All surveys were conducted by three observers (KT, BK, a local guide familiar with avifauna), who had previous experience with ornithological surveys in Papua New Guinea. We also recorded whole 15 min of point counts and unclear voices during random walks, to enable later identification (using recorder Marantz PMD 620 & Microphone Seinnheiser ME67). Observed birds were partitioned into four broad trophic guilds, namely insectivores (taking invertebrates as main food), frugivores (fruit and seed eaters), omnivores (taking plant material and invertebrates in similar ratio) and nectarivores, based on dietary information in standard references (Hoyo et al., 1992-2011, Beehler et al., 1986, Peckover and Filewood, 1976). Raptors, swifts and non-forest bird species passing through the sites were excluded from analyses. See Table S1 in Supplementary material for list of observed species, species included in analyses and their habitat and feeding preferences.

Bird diet We obtained diet samples from insectivorous and omnivorous birds by using nonlethal 1.5% potassium antimony tartarate, based on established protocols (Poulin and Lefebvre, 1995, Mestre et al., 2010). The first author examined each regurgitate under a stereo microscope and estimated the number and length of prey items eaten based on a reference collection and published order specific regressions of weight on length (Tatner, 1983, Ralph et al., 1985). Invertebrates were identified into orders. The food analyses are based on examination of prey items in 120 regurgitated samples: five from each bird species present in all study sites (i.e. *Arses insularis*, *Colluricincla* *megarhyncha*, *Meliphaga analoga*, *Melilestes megarhynchus*, *Monarcha guttula*, *Pitohui kirhocephalus*). Other bird species either did not occur in all sites or we did not manage to get the minimum of five samples thought to offer adequate representation of the diet of a species within a given time period (Sekercioglu et al., 2002). Twenty-two prey categories were identified, including 10 insect groups (Coleoptera, Diptera, Dermatoptera, Neuroptera, Odonata, Orthoptera, Hemiptera, Lepidoptera (adult), Hymenoptera were split into Formicidae, and others), Chilopoda, Lepidotera larvae, insect larvae, pupae, eggs, Araneae, Gastropoda, and vertebrates (small lizard, frog).

Habitat At each point-count point, we measured the following variables according to methods in Bibby et al. (1992): canopy height, shrub height (3 measures per point using laser measuring device); shrub foliage density (5 measures per point using scatter plot estimates; Creagh et al., 2004); percentage of ground covered by grass, bare ground and litter (15 measures in 1x1 m square per point); canopy openness (3 photos taken per point – analyzed in Gap Light Analyzer (Frazer, 1999, Frazer et al., 2001), presence/absence of fruiting trees at each point.

At each study site, we delineated three 150 x 2 m lines (between points 3-4, 6-7, 12-13) where we counted all plant stems (DBH >1 cm), and categorized them according to size (1 – 2 cm, 2 – 5 cm, and > 5 cm DBH), and leaf size (small, mid-size, large). Trees were scored as for the presence or absence of epiphytes and termite nests. Further, we counted dead logs or dead standing trees within the lines.

Prey availability survey We sampled the leaf-dwelling arthropod communities from tree saplings at all study sites. Crowns of ten tree saplings (DBH ~5 cm) were lowered above mosquito net, covered by net and sprayed with commercial insecticide. All arthropods were collected, placed in 70% alcohol and identified into the same groups as the invertebrates in food samples. All leaves were collected, weighed and their leaf area was measured using ImageJ software analysis of their digital images. Further, the mean abundance of ants was counted on 30 tuna baits (and 25 in continuous forest) placed at tree samplings after 60 minutes from exposure (J. Moses and P. Klimes, unpubl. data). Finally, abundances of butterflies were surveyed along three 300 meters long transects in all study sites. Each transect was walked slowly for 30 min, and walks were replicated ten times (P. Vlasanek, unpubl. data).

Statistical analyses We used all three survey methods to identify local species richness and bird abundances. We examined microhabitat characteristics of all sites, and eliminated those without significant differences between study sites. Namely, canopy height ($F_{3,12} = 0.98$, $P = 0.42$), mean tree DBH ($H_{3,12} = 4.67$, $P = 0.19$), fruiting and flowering trees per point ($H_{3,12} = 3.08$, $P = 0.09$), number of trees with termite nests ($H_{3,12} = 4$, $P = 0.26$) and number of dead logs ($H_{3,12} = 1.3$, $P = 0.72$) did not differ significantly between sites. Further, we used factor analysis of variables significantly different between sites to identify suites (factors) of correlated (redundant) variables. We started with six factors (shrub foliage density, shrub height, ground cover – three variables, canopy openness) and reduced the number of factors to three (explaining 86% of variability) using Kaiser-Guttman stopping rule (Jackson, 1993). From each factor, we selected a single representative variable measured in the field - litter cover, shrub foliage density, and canopy openness – and used them in following analyzes.

Using Canonical correlation in R 2.11.1 (R Core Team, 2012), we selected the species showing the strongest preferences towards continuous forest (19 insectivores, 9 frugivores, score on first axis > 0.3; CCA, first axis = continuous forest), and extracted values of representative variables (litter cover, shrub foliage density, canopy openness) from all points where our focal species were observed foraging, without respect whether the point was in fragment or continuous forest. Thus we obtained characteristics of preferred microhabitats and compared them with habitat characteristics of all points within individual study sites.

Results

We recorded 123 bird species over the course of the study at all four sites (Table S1). The overall number of forest bird species included in analyses observed at a single site varied from 80 to 107 (Fig. 2). Total species richness was higher in the continuous forest (107), than in all forest fragments (1200 ha: 84; 600 ha: 82; 300 ha: 80). Daily mist-net capture rates did not differ between sites ($t = 1.61$, $P = 0.137$). Abundance of birds recorded at each point (during 15 min, $N = 144$ per study site) was significantly lower ($F3 = 6.42$, $P < 0.001$) in the smallest fragment (19.6 ± SD 6.4), than in the other sites: mid-size fragment (21.3 ± SD 6.6), large fragment (22.1 ± SD 4.8) and continuous fragment (22.3 ± SD 5.4). The other fragments did not differ from each other and from the abundance values in continuous forest.

Similarity in species composition between sites was relatively low between the smallest fragment and both the largest fragment (Morisita - Horn index = 0.62) and the continuous forest (Morisita - Horn index = 0.59). All other comparisons revealed higher similarity between bird communities (Morisita - Horn index = 0.77 – 0.89).

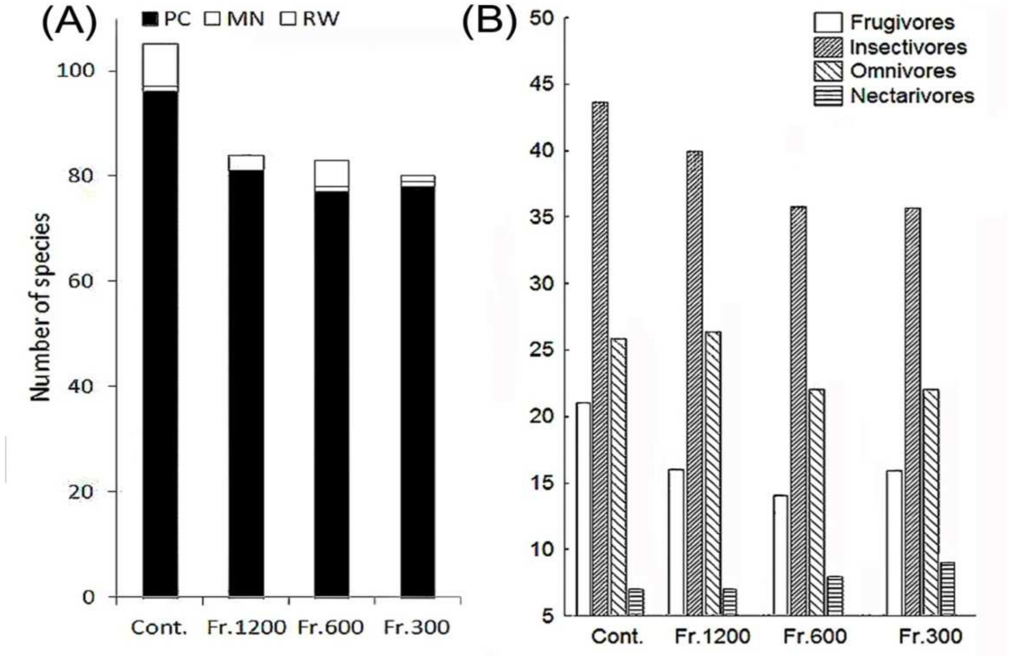

Figure 2. (A) Number of species recorded by individual survey techniques at each site (PC – point count - selected a priori as the main survey technique, MN – species recorded in mist-nets but not PC, RW – species recorded during random walks only). (B) Number of species partitioned into feeding guilds, in continuous forest (Cont.), fragment 1200 ha (Fr.1200), fragment 600 ha (Fr.600), fragment 300 ha (Fr.300) large.

The number of insectivorous bird species (35 sp.) found in the smallest fragment was lower than in continuous forest (44 sp.). Fragments of 600 and 1200 ha housed similar numbers of insectivores (37 and 39 sp.). Species richness of frugivores in continuous forest (21 sp.) was significantly higher than in all other forest fragments (1600 ha: 16 600 ha: 16, 300 ha: 14 sp.). Species richness of birds identified as omnivores did not differ significantly between the large fragment and the continuous forest, and between the medium and the small fragment (Fig. 2). Species richness of nectarivorous bird did not differ between study sites (Fig. 2)

In bird diet samples Coleoptera, Areneae, Hymenoptera (other than ants), Lepidoptera larvae, and ants (*Formicidae*) were the most common prey, comprising 62 - 71% of all food samples (Fig. 3). The relative importance of individual arthropod groups corresponded with their relative abundance found on tree saplings; however some exceptions occurred (e.g. ants or cockroaches were relatively more abundant on tree saplings than in food samples; Fig. 3). More importantly, composition of prey items in diet samples from the forest and fragments did not differ significantly for any bird species ($\chi^2 < 7.2$, $P > 0.21$; Fig. 3). The average number of prey items/diet sample did not differ significantly (Fig. 4), except samples of *Arses insularis* (Fig. 4) which decreased with fragment size.

Number of arthropod individuals per leaf area ($F_{3,36}$ = 1.15, P = 0.33) and average body length of arthropods (e.g. Araneae: $F_{3,360}$ = 1.17, P = 0.31, Lepidoptera larvae: $F_{3,111}$ = 0.2, P = 0.81, Coleoptera = $F_{3,452}$ = 0.98, P = 0.37) did not vary significantly between study sites. Similarly, there was no difference in number of adult butterflies observed along transects among the study sites (χ^2_3 = 6.66, P = 0.083), neither was there any difference in ant abundance on tuna baits ($F_{3,19}$ = 1, P = 0.40). However, more traps (17 out of 30) were visited in the 300 ha fragment than in continuous forest (9 traps) and the 1200 ha fragment (10 traps).

We found no differences in microclimate in the forest interior among study sites. None of the measured variables (average daily temperature $F_{3,29}$ = 0.76, P = 0.53, average daily humidity $F_{3,29}$ = 1.2, P = 0.32, and daily temperature fluctuation $H_{3,29}$ = 2.11, P = 0.34) varied significantly between sites.

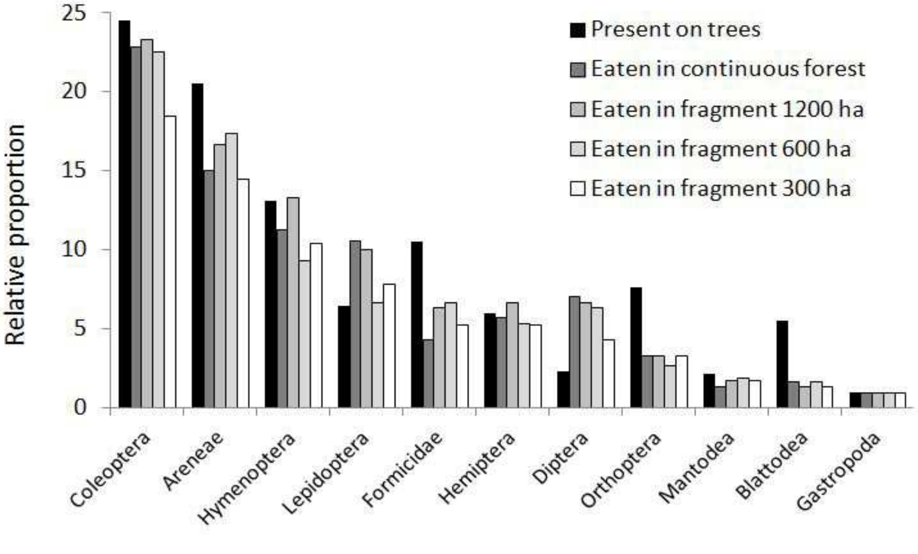

Figure 3. Mean relative importance of main arthropod taxa present on tree saplings across all study sites (there was no significant difference in number of individuals per leaf area between study sites) and in food samples of birds mist-netted in fragments and continuous forest. The differences between study sites are not significant.

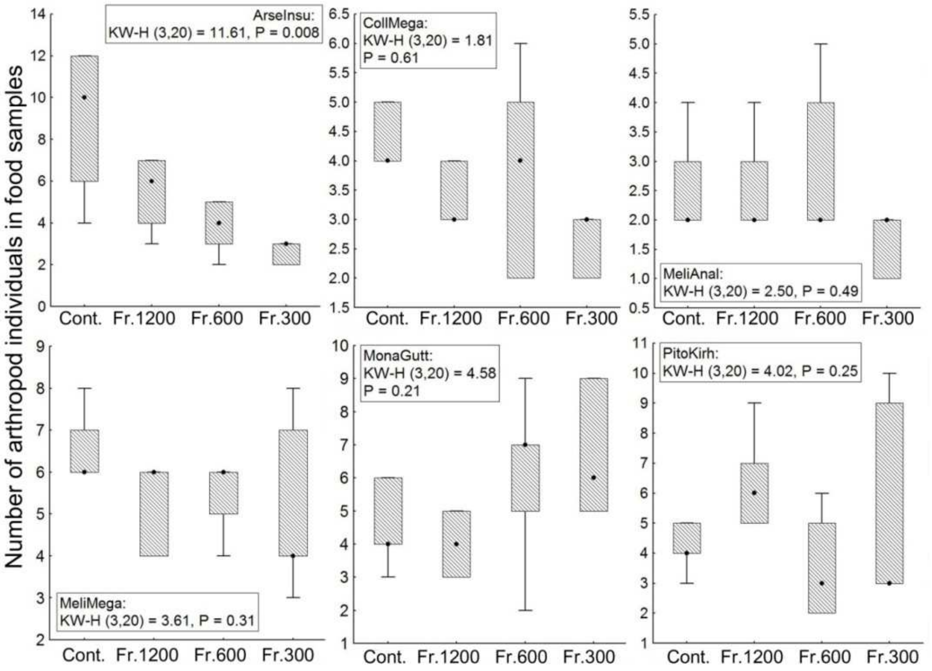

Figure 4. Number of arthropod individuals in food samples of six bird species (ArseInsu = *Arses insularis*, CollMega = *Colluricincla megarhyncha*, MeliAnal = *Meliphaga analoga*, MeliMega = *Melilestes megarhynchus*, MonaGutt = *Monarcha guttula*, PitoKirh = *Pitohui kirhocephalus*) in continuous forest (Cont.), fragment 1200 ha (Fr.1200), fragment 600 ha (Fr.600), and fragment 300 ha (Fr.300).

In general, microhabitats available in forest fragments differed from those available in continuous forest. Specifically, canopy openness in forest fragments was higher than in continuous forest, which resulted in a higher percentage of ground covered by grass (and ferns) at the expense of litter (Fig. 5). Foliage shrub density at points was more variable in fragments than in continuous forest (Fig. 5). The proportion of small (1 – 2 cm DBH) to larger (>2 cm DBH) stems was higher in the smallest fragment (33%) than in the larger fragments or continuous forest (16 – 23%), along the measured transects. Also the small stems tend to be species with larger leaves (7% small leaves, 51% mid-size leaves and 55% large leaves within 1 – 2 cm DBH category in 300 ha fragment; 22% - 28% - 29% in respectively in continuous forest). Leaf-size composition of larger plants did not differ between study sites.

We found most sensitive insectivores in points with low canopy openness (8 – 14 %), with relatively large litter cover (55 – 85 %), and shrub density between 20 – 34 % (Fig. 5). Although some points in forest fragments provided such conditions, the mean canopy openness in all fragments was higher, mean litter cover lower, and shrub density varied a lot between individual points in the fragments, and seemed to be generally lower, than on the points preferred by sensitive birds (Fig. 5).

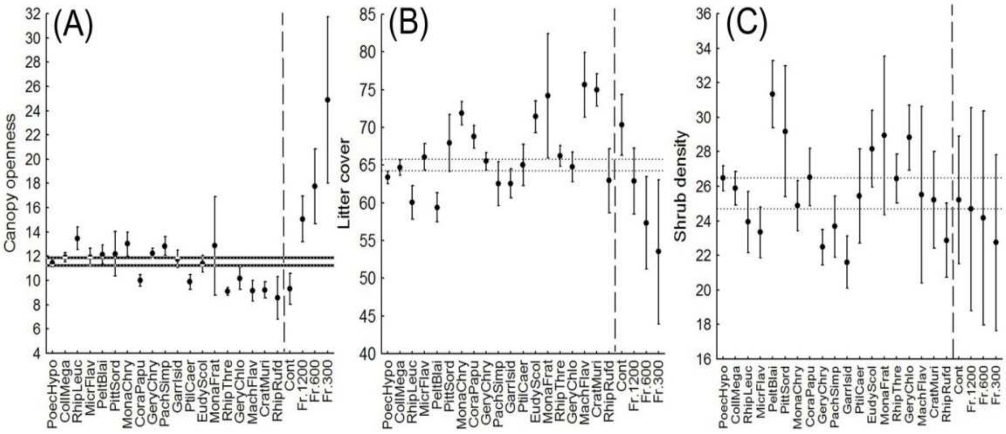

Figure 5. Microhabitat characteristics preferred by 19 sensitive insectivorous bird species: (A) canopy openness, (B) litter cover, (C) shrub density, and the mean values for these variables in continuous forest (Cont.), fragment 1200 ha (Fr.1200), fragment 600 ha (Fr.600), and fragment 300 ha (Fr.300). Means (circles), standard error (lines), and ±95% confidence intervals of means (horizontal lines). Values for birds and habitats are separated by interrupted line. See Table S1 for list of species and their name codes.

Discussion

We found fewer bird species in forest fragments, than in continuous forest. Specifically, the number of observed insectivorous bird species was the lowest in the 300 ha fragment, higher in both larger forest fragments (600 and 1200 ha) and highest in continuous forest. Also species richness of frugivores in continuous forest was significantly higher than in all forest fragments.

Food does not seem to limit local insectivorous birds in studied fragments. Arthropod richness per leaf area was similar between all study sites, and there was no obvious difference in amount of foliage across the study sites. Further, we obtained similar results from examination of bird diet, with no significant changes in food composition or in number of insects taken. Only one bird species (*Arses insularis*) had a lower number of arthropod individuals in food samples from smaller fragments. More food samples would be however needed to make a robust conclusion. Also some more subtle specificity in food preference could be underestimated by our method, since we identified prey items only to order.

The lack of support for food scarcity hypothesis in our study was in agreement with another tropical study (Sekercioglu et al., 2002) but not with three studies in the temperate zone where higher food abundance in large forest fragments was positively correlated with the abundance and reproductive performance of the two understory insectivorous bird species studied (Burke and Nol, 1998, Burke and Nol, 2000, Zanette et al., 2000).

Changes in invertebrate communities resulting from forest fragmentation are relatively well documented (Didham et al., 1996, Klein, 1989, Turner, 1996). Some studies have also shown that changes are due to the differences in food and/or microhabitat preferences: some species are unaffected or even increase their densities in fragments (Didham et al., 1996). Leaf-litter invertebrates decline as a result of desiccation in small forest fragments and generalist edge species that prefer the dense vegetation near fragment edges increase in number (Didham, 1997). Sekercioglu (2002) found that invertebrate abundance, their average length, and dry biomass in forest and fragment were surprisingly similar. We have not found any significant differences in number of arthropods per leaf area (neither per tuna bait nor per butterfly transect) in forest fragments and in continuous forest. We believe that the size of our forests can provide an explanation, as our fragments were large and we focused mainly on forest interior. Also, another study found decrease of arthropods and food shortage only in smaller fragments (~55 ha), but not in large ones (> 400 ha; Zanette et al., 2000).

The microclimate hypothesis states that sedentary understory insectivores react more unfavourably to microclimate fluctuations in forest fragments than more mobile species that are frequently exposed to different microclimates. However we failed to find significant differences in forest interior microclimate, by data loggers placed at least 300 m from forest edge.

We found that while most of the measured forest characteristics did not differ significantly between sites, the insectivorous sensitive birds foraged preferably in microhabitats that differed from those broadly available in forest fragments. Those birds were very selective towards ground cover and preferred high percentage of ground covered by litter in contrary to dense grass and fern cover. They were further seen mostly in points with small canopy openness thus small amount of light transmitted to understory. Forest fragments offered wide range of microhabitats, but only few of those points seemed to be suitable for insectivorous birds. On the other hand, continuous forest and larger fragments seemed to be more homogenous and had more points with suitable conditions. Compared to continuous forest, the understory plants of the smallest fragment had also different leaf-size composition, with relatively more plant species with larger leaves which are shown to be less attractive as searching substrate for most of the insectivorous birds (Bell, 1969).

Monarchidae, *Rhipiduridae* and *Acanthizidae* were among the bird species missing or severely influenced by forest fragmentation. Member of those families are sallying flycatchers and gleaners searching for food mainly in lower or mid storey of forests, therefore likely to be influenced by changes in their foraging substrate. Other sensitive species, e.g. *Garritornis isidorey*, Pitas or Jewel-Babblers, are dependent on forest ground substrate where they search for arthropods. This result is in concordance with a study on scrubwrens in Australia (Creagh et al., 2004), or insectivorous species in Amazonia (Stratford and Stouffer, 2013), Peru and Tensas (Marra and Remsen, 1997).

All surveys and measurements were conducted at least 150 m from forest edge, which is believed by some authors to control for direct edge effect (Didham, 1997, Laurance, 1991). Abiotic conditions (air moisture, temperature, light and soil moisture) appear to stabilize at 50 – 60 metres (Murcia, 1995) from forest edge, while canopy cover and canopy damage was impacted at least 150 m from the edge of forest fragment (Laurance, 1991). One temperate study showed that 225 ha forest fragment represented actually only 23 ha of core area (Burke and Nol, 2000), and study from North-East Queensland, reported elevated forest disturbance evident up to 500 m inside fragment margins, although the most striking changes occurred within 200 m of edges. Another study found kilometer-scale edge effects for forest beetles (Ewers and Didham, 2008). It is worth to note that 300 ha fragments, can be represented by a circle with diameter 1955 m, resulting into 71 ha of untouched forest if we consider 500 m edge effect. Our results show that the edge effect could influence birds deeper in forest fragments, supporting thus previous recommendations for 500 m distance from forest edge as buffer zones for bird point-counts (Buckland and Handel, 2006).

Sekercioglu (2002) tentatively rejected the microhabitat hypothesis, and concluded that limited dispersal capabilities of insectivorous birds may be the most important factor in their sensitivity to fragmentation. However, it is necessary to point out that he studied dispersion through cleared areas, while our study sites are surrounded by secondary growths or plantations and never by cleared areas. The New Guinean birds can be generally considered as sedentary with limited dispersal abilities (Diamond, 1973), but we were not able to test for limited dispersal hypothesis. Our observations from surrounding secondary forests (3 km from fragments) show that at least some of the species are able to wander in less suitable habitats (Tvardikova, unpubl. data), confirming thus that some of the bird species appear to be able to move through highly fragmented landscapes, but it is possible that they suffer high mortality while doing so.

Besides insectivorous birds, our surveys failed to confirm presence of some large frugivorous birds in forest fragments. Frugivorous birds not recorded in forest fragments were all large-bodied birds (Northern Cassowary *Casuarius unappendiculatus*, Purple-tailed Imperial Pigeon *Ducula rufigaster,* Cinnamon Ground Dove *Gallicolumba rufigula,* Victoria Crowned Pigeon *Goura victoria*, Coroneted Fruit Dove *Ptilinopus coronulatus*). Other species had significantly higher abundances in continuous forest (i.e. Papuan Hornbill *Rhyticeros plicatus*). None of the frugivores showed strict preference to measured habitat characteristics, and their presence did not seem to be determined by differences in number of flowering and fruiting trees and between sites during the surveys. However, we are not able to reject the possibility that canopy frugivores were missing due to seasonal movements. They all are good migrants, and suffer thus less for limited dispersal abilities able to make daily flights >10 km (Holbrook et al., 2002), following food resources across large areas. Presence of other smaller nomadic frugivores would however suggest other explanations. Also hunting for large bodied birds cannot be excluded as a possible explanation, as some villagers can hunt them on the borders of protected areas or even circumvent the ban. Restricted forest area in itself could be also responsible for absence of large frugivores. Mean home range of adult Cassowary is 206 - 213 ha (Moore, 2007), megapodes male have home range roughly 100 ha (Booth, 1987), and large, canopy frugivores, such hornbills and fruit pigeons (*Ducula, Ptilinopus*), are known or suspected to have home ranges of >100 ha (Corlett, 2009). Ranges can include both primary and secondary growths, but they are usually limited and located according to suitable nesting sites, preferably in primary forest. This could make them unlikely to stay in even large forest fragments. Decline of large-bodied frugivores has been described by some authors (Wotton and Kelly, 2012), while others did not report significant changes in their species richness in forest fragments (MacGregor-Fors and Schondube, 2011). Here we show that compared to continuous forests, species richness of large frugivorous birds decreases in forest fragments, while other frugivores did better (e.g. Eclectus Parrot *Eclectus roratus*, Brown Cuckoo-Dove *Macropygia amboinensis*).

In the view of our results, we suggest that microhabitat change influences insectivorous birds (especially litter cover, canopy openness, and foliage structure) plays important role in shaping of bird communities. We are not suggesting that these variables actually determine if birds will be present or absent, only that we identified measurable variables associated with preferred microhabitats of these birds. The direct causal factors might be prey availability or foraging efficiency, which are influenced by vegetation structure. As long as the correlative relationship between an easily measured variable (such as the density of small saplings or canopy openness) is consistent with a causal factor (such as prey density), measurement of vegetation structure is useful for describing essential elements of the habitat that must be maintained for the persistence of terrestrial insectivores.

Forest fragment of 300 ha had the most altered microhabitat conditions, most likely resulting from edge effect, which was shown to influence vegetation and forest structure deep in the forest fragments Gehlhausen et al. (2000) – 250m, Laurance (1991) – 500 m. These changes made the forest unsuitable to some of the most sensitive bird species. Neither of the larger fragments housed significantly more bird species. More research comparing foraging success, breeding and movements in both forest fragments, and altered habitats is needed to reveal the actual mechanisms of the local extinction of some lowland species in New Guinea.

Papua New Guinea is one of the few countries in the world where customary ownership of the land, originating in a tribal past, is recognized by the country's legislation (West, 2006, Sekhran, 1997), and where forest-dwelling tribal societies currently own 85 % of the land in the country (Shearman et al., 2008). Unfortunately, New Guinean communities tend to lack attitudes that favour conservation a priori. We are not aware of a single large rain forest in Papua New Guinea that has been successfully protected, and 90 % of communities opt for logging when they have opportunity to choose between this and conservation (Novotny, 2010). On the other hand, communities tend to keep a piece of forest as a source of bush-medicine, or other forest products (the case of 600 and 1200 ha fragment), or with a vision of profitable ecotourism (the case of our 300 ha fragment). Such forest fragments are sustainable for long periods even when not profitable, if they represent small percentage of land belonging to community. We show that such forest can house relatively large numbers of birds, and size of forest fragment does not have any significant effect when that fragment is larger than 300 ha. However, forest fragments larger than our study site (i.e. larger than 1200 ha) would be needed to preserve larger proportion of forest birds. While conservation of continuous forest does not seem to be sustainable despite decades of investment into conservation (Novotny, 2010), protection of larger forest fragments (~ 300 ha) could represent a useful tool, which is also the most achievable at village base.

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Supplementary material:

Table S1. List of bird species recorded at all sites during all survey, their name codes, information on habitat requirements, trophic strategies and the categorization into guild for analyzes. Ca – carnivores, Omn – omnivores, Fr – frugivores, In – insectivores, Ne – nectarivores. Raptors, swifts and non-forest bird species passing through the sites were excluded from analyses, and they are marked by asterisk in the list.

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SUPPLEMENTARY MATERIAL

Table S1. List of bird species recorded at all sites during all survey, their name codes, information on habitat requirements, trophic strategies and the categorization into guild for analyzes. Ca – carnivores, Omn – omnivores, Fr – frugivores, In – insectivores, Ne – nectarivores. Raptors, swifts and non-forest bird species passing through the sites were excluded from analyses, and they are marked by asterisk in the list.

Scientific name	Habitat	Trophic strategy	Guild
*Accipiter cirrhocephalus** **AcciCirr**	It is found in woodlands and forests, and above cleared areas.	Mainly birds caught in flight. Observed to hunt during the day, and also at dawn and dusk.	Ca
*Accipiter meyerianus** **AcciMeye**	Rain forest, forest edge and adjacent native gardens. Nesting reported in forest.	Observed to feed on birds.	Ca
*Accipiter novaehollandiae** **AcciNova**	It is found in most forest types, especially tall closed forests, including rainforests.	Feed on birds, small mammals, reptiles and large insects (*Mantoidea*).	Ca
Aegotheles bennettii **AegoBenn**	Mainly lowland forest interior and their edges.	We did not observe any feeding behaviour of the species.	Ca
Ailuroedus buccoides **AiluBucc**	We reported the species mainly of dense primary forest.	Takes insect and seeds on the ground, and lower strata. Ocassionally observed to search for food on forest floor.	Omn
Alcedo azurea **AlceAzur**	We reported the species only in the proximity of water, rivers edges and creeks, usually in shady overhanging vegetation.	Plunges from perches into water to catch prey. Prey items included: fish, crustaceans, aquatic insects and water invertebrates.	Omn
Alcedo pusilla **AlcePuss**	Observed along creeks and in tropical rainforest, creeks with dense cover, and swamps.	Feeds on crustaceans, reptiles, insects and their larvae. Makes shalow dive, which resulted in the catch of small fish.	Omn
Aplonis cantoroides **AploCant**	Inhabits wide range of natural and modified habitats, including urban areas. In forest was reported mainly from gaps, and forest edges with flowering trees.	Takes mainly fruits (figs, fruit from forest palms). Hawks flying insects. Forages in pairs and small flocks. We reported about 10% of the flocks to be mixed with *Aplonis metallica*.	Omn
Aplonis metallica **AploMeta**	In Madang, we reported the species in rainforest, coastal woodland, mangroves, also forest edge and clearings, gardens.	Mainly frugivorous (figs, and palm seeds); also takes nectar, some insects. Large flocks observed on flowering trees.	Om
Arses insularis **ArseInsu**	Rainforest in lowlands. Also on forest edge, but seems to avoid disturbed habitat.	Primarily insectivorous. Forages mainly in middle stratum among large trees (10-15 m), but often ascends to lower canopy and occasionally descends to thickets.	In
Cacatua galerita **CacaGale**	Found in variety of forest areas such as secondary growth, woodland (including swamp and riverine), mangroves, open country, agricultural land.	Forages on grasses and herbs. Other foods include: roots, nuts, berries, flowers, blossoms and very ocassionally insect larvae.	Fr
Cacomantis variolosus **CacoVari**	It is found in wooded habitats, including rainforest, wet forests, along waterways and in more open forests and woodlands. Sometimes in gardens.	Eats insects, particularly hairy caterpillars. It usually forages high in the forest canopy but may sometimes feed on the ground.	In
Caliechthrus leucolophus **CaliLeuc**	Forest, mainly canopy in hilly country.	Mainly insects, including caterpillars, other arthropods; also fruit. Feeds in canopy.	In

Campochaera sloetii **CampSloe**	Primary forest and forest edge of small clearings.	Eats mostly fruit and insects. Occurs in pairs or small parties in upper canopy and outer foliage. Obtains food by gleaning.	Omn
Casuarius unappendiculatus **CasuUnap**	Reported only in flat lowland primary forests. Regularly following watercreaks, where the species was reported usually in the mornings.	Feeds on large fruits collected from forest ground.	Fr
Centropus menbeki **CentMenb**	Forest, forest edge, srub and lower middle storyes.	We reported mainly large insects (grasshoppers, cicadas, caterpillars), and other arthropodes, and mall vertebrates (snakes, frogs). Feeds on ground, where movements clumsy, and in vines.	Omn
Centropus phasianinus **CentPhas**	Prefers dense understorey vegetation, particularly grasses, rushes, bracken and sedges, in open forests and woodlands, and around wetlands. Often found feeding on gardens with thick grasses.	Feeds on the ground on large insects, frogs, lizards. Eggs and young of birds and, sometimes, small mammals were reported by other authors, but we did not observe such behaviour.	Omn
Ceyx lepidus **CeyxLepi**	Primary and secondary forest, thick vegetation along stream rivers. However, it is not dependent on water and was found in habitats far away from creaks.	Insect, and small frogs and tadpoles. Sits on low branches, flies usually in lower strata, and is very common in mist-nets below 3 m.	In
Chaetorhynchus papuensis **ChaePapu**	Typical bird of forest interior. Previously was reported from altitudes 200 - 1600 m a.s.l., mainly 600 - 1400 m a.s.l.. Here we report the species to occur in primary forest at 150 - 200 m a.s.l..	Feeds on insect and spiders. Hunts in middle stage of forest, and captures prey by sallying.	In
Chalcophaps stephani **ChalStep**	Inhabits humid evergreen forest interior and dry secondary coastal forest. Some authors reported sympatric occurence with C. indica, but C. indica occupying forest edges and C. stephani edges at that case. We mist-netted both species in forest interior in the forest fragment 300 ha large, but C. stephani was much more abundant in continuous forest.	Spend most of the time on the ground, taking seeds, fallen fruits and probably insect.	Fr
Charmosyna placentis **CharPlac**	In Madang district, was found primary forest, forest edge, tall secondary growth, swamps, and coconut groves .	Feeds on pollen, nectar, flowers and seeds.	Fr
Chrysococcyx minutillus **ChryMinu**	Lowland forest and forest edge, monsoon forest, swamp forest, secondary growth.	Insect, mainly caterpillars, also beetles and bugs. Forages in canopy.	In
Cicinnurus regius **CiciRegi**	Lowland rainforest, and forest edge, including tall secondary forest.	Mainly takes fruits and only sometims arthropods. Forages at various levels of forest.	Omn
Cinnyris jugularis **CinnJugu**	Occurs mainly in forest edges, flowering trees, forest gaps and clearings.	Nectarivorous, taking also small insect.	Ne
Colluricincla megarhyncha **CollMega**	Inhabits rainforest, monsoon forest, ecologically disturbed habitats, tall secondary growth.	Food is mainly insects, spiders, small snails, and occasionally fruit, obtained mostly by gleaning.	In
Coracina boyeri **CoraBoye**	Forest, forest edge, tall secondary growth, partly cleared areas and locally	Eats mainly fruit, especially figs, but takes also insect.	Omn

	mangrove forest.	Forages mainly in upper canopy.	
Coracina melas **CoraMela**	Rainforest and monsoon forest; locally also gallery and mangrove forests; normally in forest interior, but visits edges and adjacent secondary growth, disturbed areas.	Feeds mainly on adult and larval insects, including caterpillars; also takse fruit. Foraging in subcanopy and lower trees also.	In
Coracina papuensis **CoraPapu**	Many vegetation types, rainforest, forest edges, secondary growth, mangrove, coconut plantations, in Madang province.	Mainly larger insect. Also known to take fruit and seeds od plant as fig, acacia and grasses. Food obtains mainly by gleaning.	In
Coracina tenuirostris **CoraTenu**	We reported the species mainly of forest interior. Observed to search in mid-storey and upper-strata.	Food samples included caterpillars.	In
Corvus tristis **CorvTris**	Primary rainforest, forest edge, secondary growth, gardens. Very often visits open areas and riverbanks, and flies above walleys.	Feeds mainly on fruits in forest canopy; also takes insects, and sometimes scavenges on forest floor. Gleans in foliage and also on ground.	Omn
Cracticus cassicus **CracCass**	Lowland forest and dense second growth. Occurs in openings in rainforest, forest edge and gardens.	Feeds on large insects, larvae, spiders and fruit; also taken small vertebrates, including birds. Forages mostly in crowns of trees bordering open spaces.	Omn
Cracticus quoyi **CracQuoy**	Occurs in most forest types and plantation in lowlands. Sometimes feeds by pouncing to the ground, but in forest forages mostly in higher strata.	Invertebrates, mainly insects; also small vertebrates, e.g. small lizards and snakes, frogs, small mammals and birds (including nestlings), small crabs and fish; also some fruit.	Omn
Crateroscelis murina **CratMuri**	Primarily hill forest, from 460 m, occurring in lower mountains to c. 1700 m. Occupies a terrestrial and low-level strata, understorey and shrubs, sometimes in dense areas but also in open places. Previous studies reported occurance above 460 m, here we report on range extension to much lower altitudes at 100 m a.s.l.	Diet consisted only from rthropods. Usually was seen singly or in pairs; sometimes in family groups. Forages low in understorey, on sides of trees. Glean from undersides of leaves.	In
Cyclopsitta diophthalma **CyclDiop**	Found in variety of areas including rainforest, secondary growth forest, forest edge, riverine forest, and other open areas.	Seeds are main food item; also small whole fruits, nectar was observed to be taken. Other authors reported insect larvae, but our data can't confirm this.	Ne
Dacelo gaudichaud **DaceGaud**	Mainly in lower canopy of riverine forest, and primary rainforest, very abundant in tall secondary growth. Reported mainly from high trees.	Arthropods, also small vertebrates, such as frogs, lizards. Bones of small bird or mammal also reported.	Omn
Dicaeum geelvinkianum **DicaGeel**	Forest canopy and edge, particularly around flowering and fruiting trees, also secondary growth, plantations and gardens.	Nectar and pollen, fruits and seeds and spiders also taken occasionally. Forages in canopy and upper atrata.	Ne
Dicrurus bracteatus **DicrBrac**	Species inhabits mainly open areas with high trees, and higher strata of gallery forests. Occurs also in forest gaps in primary forests.	Insectivorous	In

Ducula pinon **DucuPino**	Inhabits forest, and partially cleared areas.	Frugivorous, searching in canopy.	Fr
Ducula rufigaster **DucuRufi**	Forest and sometimes forest edge.	Frugivorous, the most important were *Arecacea*, *Myristicae*, *Lauraceae*. In lower canopy.	Fr
Ducula zoeae **DucuZoea**	Inhabits rain forest.	Feeds on various fruits including *Arecaceae*, *Lauraceae*, *Annonaceae* and *Moraceae*. Feeds in canopy in small flocks of up to 10 birds.	Fr
Eclectus roratus **EcleRora**	Found in wide range of habitats from forest to secondary growth forest, and coconut plantations.	Consists of fruits, berries, nuts, seeds of eucalypts and acacias in particular; nectar, leaf buds and blossoms.	Fr
Eudynamys scolopaceus **EudyScol**	Forest interiors and only ocassionally forest edges.	Consuming a variety of insects, small vertebrates and various fruits. We reported fruits to be taken only ocassionally, other authors identified the species as omnivorous.	In
Eurystomus orientalis **EuryOrie**	Inhabits open wooded areas, with mature, hollow-bearing trees suitable for nesting. Daytime spends pearching on emergent or dry standing trees in open ares (gardens, forest gaps).	Feed almost exclusively on flying insects. They search for food from a conspicuous perch and then capture it in skilful aerial pursuits.	In
Gallicolumba rufigula **GallRufi**	Primary rain forest.	Diet consists of seeds, fallen fruits and insect. Considered to be more insectivorous than C. indica and C. Stephani.	Fr
Garritornis isidorei **GarrIsid**	We recorded the species mainly in primary forest, and on edges of small gaps.	Forages mainly by probing bark and on trunks and branches, also digs in litter of jungle floor very often. Diet includes a range of arthropods; small reptiles are also taken.	In
Geoffroyus geoffroyi **GeofGeof**	Found in primary and secondary forests, plantations, open woodland, mangrove and gardens.	Feeds on nectar, seeds, fruit and blossoms.	Ne
Gerygone chloronota **GeryChlo**	In dense forests and thickets, mainly in primary forest and also tall secondary growths.	Prey includes spiders (Araneae), cockroach egg sacs (Blattodea), beetles (Coleoptera), bugs (Hemiptera), wasps (Hymenoptera) and lepidopteran larvae.	In
Gerygone chrysogaster **GeryChry**	Rainforest, secondary growth, monsoon forest and riparian formations.	Insectivorous, but no details of prey.	In
Goura victoria **GourVict**	Occupies swamp and large primary forests, as well as drier forests, only in the extreme lowlands.	Diet consists of fallen fruit, berries and seeds. Occasional snail and possibly ground-dwelling larger insect. Forages on the forest floor in groups of two to ten individuals.	Fr
*Haliastur indus** **HaliIndu**	Terrestrial wetlands and urban areas, in tropics ranges over forest, farmland and grasslands. In primary forests reported mainly along river banks and large clearings. Nets usually at high tree close	Variety of small animals and carrion, including mammals, birds, reptiles, amphibians, fish, arthropods. Quite often also domestic poultry.	Ca

	to river. Two nests reported on high dry trees in the middle of large cleared garden.		
*Haliastur sphenurus** **HaliSphe**	Lightly wooded and open areas, typically near or over terrestrial and marine wetlands.	Variety of small animals and carrion, including mammals, birds, reptiles, fish, crustaceans, insect.	Ca
*Harpyopsis novaeguineae** **HarpNova**	Local in large primary forests, but visits nearby clearings and native gardens. Nests reported only in forest. No individuals reported in further distance from forest, in larger open areas.	Mainly terestrial and arboreal mammals, including cuscus, possum, wallabies, tree-kangoroos, giant rats. Possibly young dogs and pigs (reported by villagers). Also birds and reptiles, including snakes and monitor lizards. Forages from series of perches.	Ca
Hemiprocne mystacea **HemiMyst**	High emergent crowns, scattered trees, and edge of large forests. Ocassionally reported in gaps.	Takes flying arthropods, including bees, ants, hemipteran bug and beetles.	In
*Henicopernis longicauda** **HeniLong**	Tropical rain forest, forest edge, and adjacent clearings. One nest found in forest	Mostly takes insect, including wasps and their larvae, also lizards, small birds and content of their nests, and small mammals. Forages close to forest canopy, or between tree trunks.	Ca
Lalage atrovirens **LalaAtro**	We reported the species mainly in forest interior, and on high trees in clearings.	Eats mostly fruit but we reported also insects. Food obtains by gleaning and by “flycatcher-gleaning”.	Omn
Leptocoma sericea **LeptSeri**	Species of edges, where flowering trees are presents. Possibly also canopies. Present in both primary and secondary forests.	Food includes pollen, nectar, floweres and soft fruits. We did not find any insect in food samples.	Ne
Lonchura tristissima **LoncTris**	Species was reported in grasslands, along river banks in primary forest, and in gardens or small gaps.	Diet mainly consists of grass seeds and weeds.	Fr
Lorius lory **LoriLory**	Found in primary forest and forest edges, also has been recorded in well grown secondary forest. Also occurs in partially cleared areas.	Includes pollen, nectar, flowers, fruit and insects.	In
Machaerirhynchus flaviventer **MachFlav**	Rainforest, gallery forest, thick secondary growth and forest edge.	Food insects. Seen singly or in pairs; often a member of mixed-species feeding flocks.	In
Macropygia amboinensis **MacrAmbo**	Forest edges in gallery woodland, isolated tree groups an grasslands, forest secondary growth and gardens.	Small fruit, seeds and nuts, grass seeds have been recorded in food samples. Small stones reported also in food samples. It is found feeding in middle to canopy.	Fr
Manucodia chalybatus **ManuChal**	We reported the species mainly in forest interior, and on high trees in clearings.	Mainly fruits, especially figs; also invertebrates, including insects and spiders (Araneae). Forages mostly in middle to canopy levels.	Omn

Megapodius decollatus **MegaDeco**	Rain forest interior, usually along riverine flatlands.	Searches for insect in litter, and high proportion of food is represents fallen fruits.	Omn
Melanocharis nigra **MelaNigr**	Dense vegetation in primary rainforest, and dense secondary growth. Nests found usually above 10 - 15 abuve ground in forest interior, but not dense shrubs.	Insect. Forages in mid-storey, and in lower strata.	In
Meliphaga analoga **MeliAnal**	Primary forest and forest edge, secondary forest, tall secondary growth, scrub and scrub-forest, also riparian and roadside vegetation, in some areas also coffee plantations, gardens and garden trees at forest edge.	Diet includes arthropods (insects), fruit, seeds (probably ingested with fruit), and nectar from flowering trees (including Syzygium). Insect also found in food samples.	Omn
Meliphaga aruensis **MeliArue**	Variety of forest habitats, including primary rainforest and low plains forest, also disturbed habitats such as forest edge, secondary forest and tall or old regrowth.	Diet includes fruit, seeds (probably ingested with fruit), and arthropods (mainly insects); probably also nectar, and known to visit inflorescences of Poikilospermum and Syzygium. Mainly in understory, lower middle story.	Omn
Melidora macrorrhina **MeliMacr**	Lower primary and secondary rainforest, gallery forest, scrub-forest, also partly cleared areas, isolated groups of trees.	Large insect, including stick-insect, also frogs.	In
Melilestes megarhynchus **MeliMega**	Dense vegetation in primary rainforest, forest edges, tall riparian forest and secondary growth, and other disturbed habitats.	Small arthropods, nectar, occasionally fruit. Forages at all hights, mainly in lower and middle storey, less often in canopy.	In
Microeca flavovirescens **MicrFlav**	Mostly in interior of primary forest.	Insects including weevils and other beetles (Coleoptera) and Hymenoptera.	In
Micropsitta pusio **MicrPusi**	Found in many habitats, in canopy of primary forest or in edges of forest fragments. Also in clearings with high trees.	Feeds while gripping upside down on the sides of tree trunks, tail braced as a prop. Takes mostly fruils, nectar but also insects.	Ne
Mino anais **MinoAnai**	Tall primary forest, forest edge and partially cleared areas, provided that tall trees still present.	Diet apparently only fruit. Forages primarily in upper canopy.	Omn
Mino dumontii **MinoDumo**	Forest of various types, including rainforest, swamp-forest; also forest edge and partly cleared areas.	Diet mainly fruit, also insects. Often feeding on fruit and berries. Also gleans caterpillars or hawks insects from high perches.	Omn
Monarcha chrysomela **MonaChry**	Forest, including monsoon forest, hill forest and gallery forest, usually along edges, clearings and treefall areas.	Food largely small invertebrates, including grasshoppers (Orthoptera).	In
Monarcha frater **MonaFrat**	Mainly forest interior, but also forest edges and secondary forest.	Food items mostly small to medium-size invertebrates. Forages and gleans insects from within canopy of middle levels of forest trees.	In
Monarcha guttula **MonaGutt**	Interior of primary and secondary forest; however more common in primary forest. Secondary growths only	Food items mostly small invertebrates and larvae. Search in shrubby and shaded	In

	those old and tall.	lower and middle levels af forest trees.	
Monarcha manadensis **MonaMana**	Mainly in forest interior.	Insectivorous, hunting in mid-storey, understorey.	In
Monarcha rubiensis **MonaRubi**	Lowland rainforest and swamp forest, usually in forest interior.	Food mainly small to medium-sized invertebrates. Forages among foliage of lower to middle level of trees.	In
Myiagra alecto **MyiaAlec**	Primary forest, forest edges, streamside vegetation, secondary growth; usually in vicinity of water, but will visit forest patches.	Largely insectivorous; some fruit, small molluscs and crustaceans may be taken. Tends to keep to middle and low levels in dense vegetation.	In
Myzomela eques **MyzoEque**	Primary rainforest, forest edge and tall secondary forest and regrowth, found in lowland alluvial rainforest and edge.	Primary nectar, from wide range of flowering plants, including figs, also insect and reported as eating plants. Forages mainly in outer canopy of tall flowering trees, also in vines and epiphytes, less often in lower canopy, subcanopy or mid-strata.	Ne
Oedistoma iliolophus **Eodillio**	Interior of primary forest.	Insect and nectar. Forages in mid-strata.	Omn
Oriolus szalayi **OrioSzal**	Mainly disturbed areas, forest edges and second growth, swamp forest, gallery forest and scrub.	Fruits, insect, also some grass seeds and probably nectars. Mainly in canopy.	Omn
Pachycephala hyperythra **PachHype**	Previously reported from forest interiors at altitudes 400 - 1200 m, locally to 1400 m, being replaced, with considerable overlap, by P. simplex in lowlands and by P. soror at higher elevations. We reported the species to be present at much lower altitudes (100 - 200 m a.s.l.) in all surveyd primary forests; however in low abundances.	Insects. Prey captured by gleaning in undergrowth (c. 30%) and lower storey (c. 70%), mainly on the trunk and branches in inner two-thirds of trees.	In
Pachycephala simplex **PachSimp**	Inhabits rainforest, tall secondary growth, forest edges, only partly cut forest or dense second growth.	Insects. Gleans prey mainly in lower to middle storeys of forest; forages also at tops of saplings in clearings.	In
Paradisaea minor **ParaMino**	Primary forest, swamp-forest, forest edge and second growth; adaptable to human-altered environments. Adult and subadult males restricted to forest and advanced second growth, whereas birds in female-type plumage have broader variety of disturbed habitats.	Mostly fruits, also arthropods. Forages mainly in canopy; also lower when seeking arthropods.	Omn
Peltops blainvillii **PeltBlai**	Canopy of lowland rainforest, especially at openings and edges; three falls, road verges and river edges and another disturbed areas, such as gardens.	Mainly flying insects, including dragonflies.	In
Philemon buceroides **PhilBuce**	Rainforest, forest edge, swamp forest, tall and dense secondary growth and other disturbed areas, such as sides of roads and tracks.	Fruit, nectar and insect. Mainly in uppers canopy. Often on flowering trees.	Omn
Philemon meyeri **PhilMeye**	Rainforest, forest edge, swamp forest, tall and dense secondary growth and other disturbed areas, such as sides of	Fruit, nectar and insect. Mainly in uppers canopy, at times descending to upper levels of	Omn

	roads and tracks.	middle stage of lower in dense secondary growth.	
Pitohui dichrous **PitoDich**	Forest, forest edges and secondary growth, occasionally mangroves and low beach trees.	Mainly fruit, including small figs (Ficus); some insects and grass seeds.Found at most levels, from undergrowth to canopy.	Omn
Pitohui ferrugineus **PitoFerr**	Rainforest, monsoon forest, gallery forest, tall secondary growth, sometimes extending into disturbed areas and plantations adjacent to forest.	Insects and fruit. Frequents understorey to lower canopy.	Omn
Pitohui kirhocephalus **PitoKirh**	Forest edges, tall secondary growth, disturbed forest, primary rainforest, swamp-forest, gardens.	Insects and fruit. Ranges from understorey to canopy; often hides in dense vegetation.	Omn
Pitta erythrogaster **PittEryt**	Found in many habitats, from dense primary rainforest to logged or heavily degraded forest and scrub, plantations, remnant forest patches within cultivations, and thickets near rivers.	Takes insects and their larvae, e.g. small beetles, also snails, earthworms, and even green plant material and seeds. Forages on forest floor, mainly by gleaning on litter.	In
Pitta sordida **PittSord**	Occupy especially primary riverine forest, secondary forest with heavy understorey or scrub, wet or dry forest, also peatswamp-forest.	Insects of many kinds, e.g. beetles, ants, termites (Isoptera), Orthoptera, cockroaches (Blattodea), bugs (Hemiptera), various larvae; also earthworms and snails. Forages on forest floor among litter.	In
Poecilodryas hypoleuca **PoecHypo**	Rainforest, swamps forest with sago palm. Locally reported in secondary growth, particularly where sympatric with *P. brachyura*.	Insects. Most common in lower understorey, usually within a few metres of ground, occasionally up to 15 m in studies. Prey obtained mostly by gleaning.	In
Probosciger aterrimus **ProbAter**	Primary rain forest.	Feed on seeds, nuts, berries , and fallen fruits that they may find, but they would rather eat plants than fruits. They also eat insects, and insect larvae.	Fr
Pseudeos fuscata **PseuFusc**	Prefers humid forest margins, secondary growth, savanna, plantations and some inhabited areas.	Feeds on flowers, fruits and insects.	Fr
Psittaculirostris edwardsii **PsittEdwa**	Found up to 800m in humid lowland forest, partially cleared areas, forest edge as well as near human settlements.	Feeds on fruits, figs, casuarinas, nectar. We did not confirm any insects to be taken.	Fr
Ptilorrhoa caerulescens **PtilCaer**	Rainforest, monsoon forest, adjacent tall secondary growth and gallery forest; prefers damper localities.	Forages on ground for insect; uses bill to turn leaves, and probes in crevices.	In
Ptilinopus coronulatus **PtilCoro**	Inhabits rain forest, secondary forest and edge, monsoon forest and in some areas gallery forest.	Frugivorous, feed on variety of fruits, particularly figs, laurel and palms. Feeds at al levels from undestorey to upper canopy.	Fr
Ptilinopus iozonus **PtilIozo**	Inhabits a variety of forest types and wooded open areas. One of the most common Fruit Dove in many habitats aorun Madang lowlands. Seen in large	Feed on fruits, mainly on figs (84%).	Fr

	flocks in open areas and forest edges.		
Ptiloris magnificus **PtilMagn**	Lowland forest, swamp-forest, and gallery forest and forest edge. Occasionally in mangroves and plantations.	Fruits and animals, latter including wide variety of insects, spiders and myriapods. Overall a greater proportion of arthropods eaten, but relative proportions vary seasonally. Forages mostly in main canopy for fruits, but gleans/probes for insect.	Omn
Ptilinopus perlatus **PtilPerl**	Found in lowland rainforest, quite common along river courses.	Feed on fruit, especially figs	Fr
Ptilinopus pulchellus **PtilPulc**	In primary and secondary forest.	Diet consists mainly of various fruits from trees, palms and vines.	Fr
Ptilinopus superbus **PtilSupe**	Found in rainforests, rainforest margins, mangroves, wooded stream-margins.	Feed almost exclusively on fruit, mainly in large trees.	Fr
Ptilinopus magnificus **PtilMagn**	The most favoured habitat is rainforest, and birds are rarely seen in other areas. The birds do not travel large distances, but move around in small, localised areas in search of fruit-bearing trees.	Feed on a variety of rainforest fruits.	Fr
Reinwardtoena reinwardtii **ReinRein**	Very common species of many habitats with high trees.	Feeds on variety af small seeds and fruit, pebbles found in some stomachs. Comes to ground periodically to feed.	Fr
Rhipidura leucothorax **RhipLeuc**	Variety of habitats, including scrub, secondary growth fringing waterways, forest edges of mangroves, also gardens. Usually doesn't enter forest intrior of primary forest. *Rhipidura* species of the most open habitats.	Insect, nestling diet includes butterflies and moths. Forages usually within a few meters of the ground. Gleaning 40%, and flycaching 20%.	In
Rhipidura rufidorsa **RhipRufd**	Rainforest, monsoon forest, nerby tall sedentary growth and swamp-forest. Mainly in interior of forest, sometimes on edge.	Insect. Forages from near ground levet to canopy, but mostly in lower to middle levels. Mostly gleaning on leaves (on growth up to 2 m, 80% of our observations), but also leaf litter.	In
Rhipidura rufiventris **RhipRufv**	In a range of forest habitats from primary rainforest to tall secondary forest. Often in more open areas than *R. threnothorax* and *R. rufidorsa*.	Insectivorous. In New Guinea reported to be 7% of feeding at 0-1m, 10% at 1-2m, 26% at 2-4m, 16% at 4-6m, 19% at 8-12m.	In
Rhipidura threnothorax **RhipThre**	Primary forest interior. Particularly dense undergrowth in deep shade, avoiding direct sunlight.	Small insect, restricted to understorey. Usually no more than 2 m from ground. Food items gleaned from leaf litter on ground and on branches.	In
Rhyticeros plicatus **RhytPlic**	Occurs throughout lowland forests (primary nad secondary). Nests are placed on high trees, and species seem to be limited by their presence. Few times was reported to over-fly smaller fragments, and secondary growths, but we never repoted the species to used	Its diet consists mainly of fruits, especially figs (Ficus). Occasionally supplemented with large insects and other small animals.	Fr

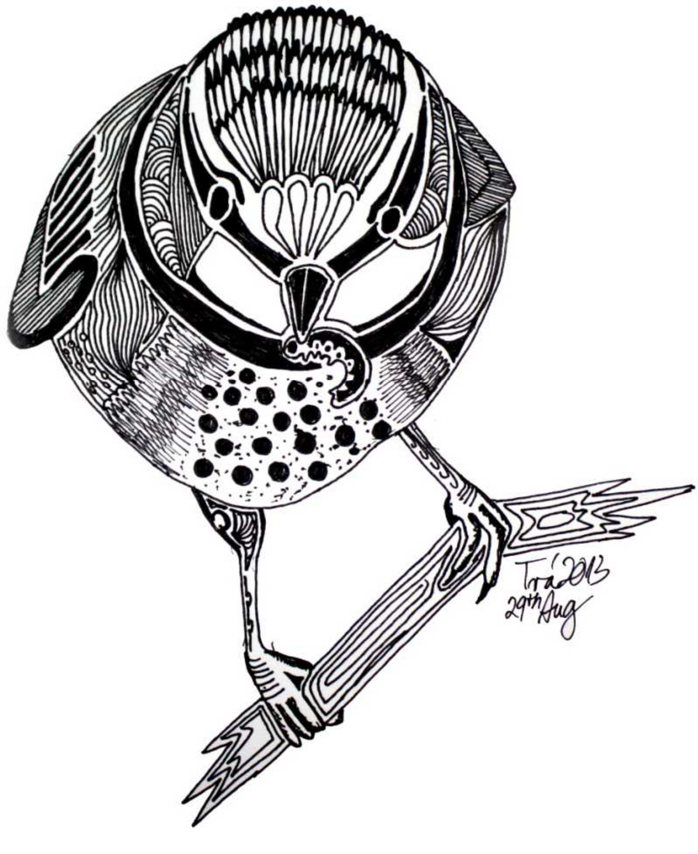
	such habitat activelly.		
Sericornis spilodera **SeriSpil**	Found in dense interior of primary forest only. Mist-netting reveald the species occur mostly in understory, but reported to ascend to 15 m in dense patches with high saplings.	Exclusively insectivorous. Keeps quiete low in understorey but will ascend to middle level; gleans actively from leaves, twigs and branches.	In
Syma torotoro **SymaToro**	Species of interior of primary forests. Seems to avoin open areas.	Insect, larvae, and small lizard.	Omn
Talegalla jobiensis **TaleJobi**	Seems to prefer dry ground, in flat area, and avoind swampy forests. However, quite often found to search in previously flooded habitat along river banks. Nest never found there.	Orbserved to take fruits, as the main food. Possibly also takes larger insects found in litter.	Fr
Tanysiptera galatea **TanyGala**	Primary lowland rainforest but also found along watercourses in grassy valleys, and in forest fragments, and in secondary forest. Dependent on presence of arboreal termites.	Takes many different arthropodes, also Gastropoda, Coleoptera, Orthoptera, Lepidoptera, Chilopoda and small lizards.	Omn
Toxorhamphus novaeguineae **ToxoNova**	We reported the species mainly in interior of primary forest.	Insect and nectar. Forages in mid-strata.	Fr
Trichoglossus haematodus **TricHaem**	Occupies wide variety of areas including settlements, forest, coconut plantations, savanna, eucalypt stands and mangroves.	Feeds mainly on nectar but will also take figs, insects.	Omn
Xanthotis flaviventer **XantFlav**	Mainly dense lowland rainforest, forest edges, remnant forest patches, and secondary rainforest forest.	Mainly insect, including beetles, grasshoppers, cockroaches, cicadas and caterpillars, also nectar and fruit. Forages at all levels, mostly in upper canopy.	Fr

Chapter VI

Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea

Katerina Tvardikova, Vojtech Novotny

Journal of Tropical Ecology (2012) 00:1–11



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Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea

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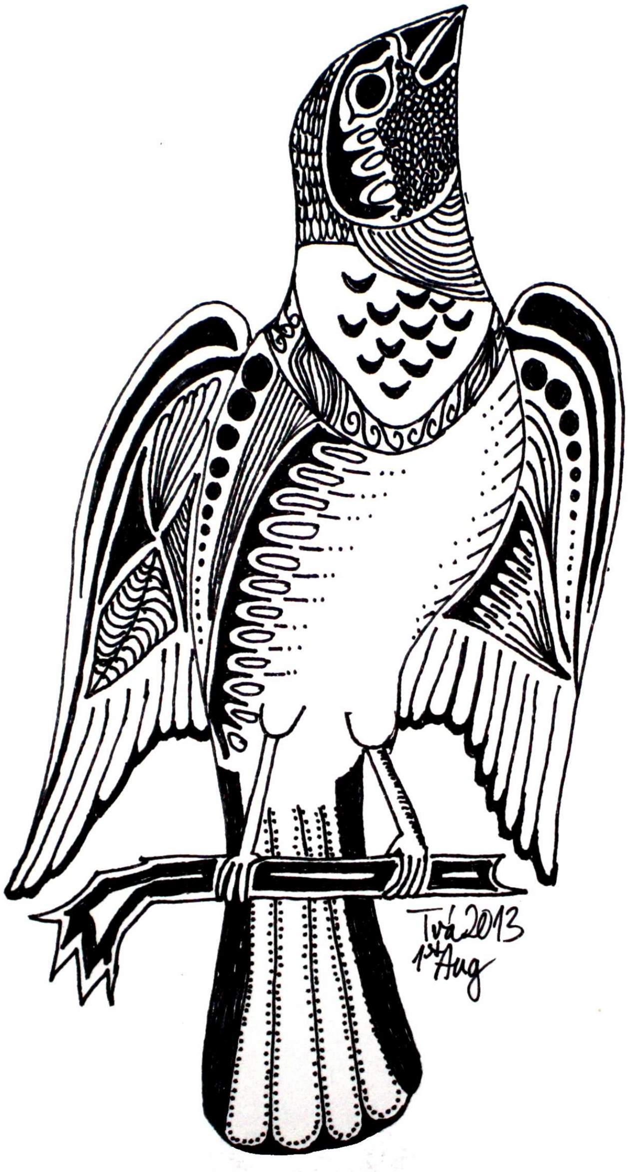
Abstract: Although predation is generally seen as one of the key factors determining the abundance and composition of insect herbivore communities in tropical rain forests, quantitative estimates of predation pressure in rain-forest habitats remain rare. We compared incidence of attacks of different natural enemies on semi-concealed and exposed caterpillars (Lepidoptera) in lowland and montane tropical rain forests, using plasticine models of caterpillars. We recorded attacks on caterpillars in four habitats: primary forest, secondary forest and forest fragment in lowlands (200 m asl), and montane primary forest (1700 m asl). We used 300 exposed and 300 semi-concealed caterpillars daily, and conducted the experiment for 6 d in every habitat. Daily incidence of attacks was higher on exposed caterpillars (4.95%) than on semi-concealed (leaf-rolling) caterpillars (2.99%). Attack pressure of natural enemies differed also among habitats. In the lowlands, continuous primary and secondary forests had similar daily incidence of attacks (2.39% and 2.36%) which was however lower than that found in a primary forest fragment (4.62%). This difference was caused by higher incidence of attacks by birds, ants and wasps in the forest fragment. The most important predators were birds in montane rain forests (61.9% of identified attacks), but insect predators, mostly ants, in the lowlands (58.3% of identified attacks). These results suggest that rapid decrease in the abundance of ants with altitude may be compensated by increased importance of birds as predators in montane forests. Further, it suggests that small rain-forest fragments may suffer from disproportionately high pressure from natural enemies, with potentially serious consequences for survival of their herbivorous communities.

Key Words: ants, birds, Lepidoptera, model caterpillars, parasitoids, predation pressure, primary, rain forest, secondary

SUMMARY and APPENDICES

Katerina Tvardikova



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SUMMARY

This thesis explored the diversity and ecology of forest bird communities in diverse tropical forests in Papua New Guinea. Altogether, there is about 485 bird species occurring in forests on the mainland of New Guinea. From those, I managed to record 260 bird species along altitudinal gradient and 152 bird species across various lowland sites during the course of my field work. For most of them, ecological requirements are poorly known.

A typical square kilometre plot of lowland rainforest in New Guinea supports roughly 150 bird species, and about 120 - 130 typically forest species in forest interior. With an approximate figure of 150 species, the Papuan list is comparable to a site in Indonesia, richer than forest in West Africa, but very much poorer than a variety of sites in Amazonia, where local lists commonly exceed 350 species (Beehler *et al.* 1986). While the lowland and hill forests communities are the most species rich, the forest at higher altitudes become gradually species poor, and tops of the mountains host about 30 - 40 species.

With respect to avian guilds, I found that forests of New Guinea support relatively low proportion of frugivores (40% identified as mixed-feeders taking both fruits and some insect – *Chapter III*, 34.5% of birds identified as “mainly frugivores” along the altitudinal gradient – *Chapter I*, but only 8% identifies as strict fruit feeders – *Chapter III*). This includes members of obligate frugivores (genus *Ducula* and *Ptilinopus*), relatively uncommon in other parts of the world, and occurring mostly in New Guinean lowlands.

New Guinean assemblages of ground-feeding forest birds are likewise considerable. With cassowaries, megapodes, large ground pigeons, and forest rails, it appears that there has been a considerable radiation, maybe thanks to missing large ground vertebrates and ground predators.

Insectivorous birds in New Guinea are very species rich, showing all kinds of segregation, and allowing thus high species richness at local scales. Altitudinal segregation (in many genera, two or more species forage in similar ways at different altitudes), habitat segregation (e.g. uniform species of genus *Gerygone* subdivide lowland habitats) or vertical stratification of forest strata (e.g. genus *Rhipidura*) are among the most common.

On the other hand, surprising gaps exist in composition of the Papua avifauna. For example, the remarkable ant-following guilds known from Neotropics are absent in New Guinea. The “woodpecker” niche is only partly filled by some bark-gleaning species (various birds of paradise, sittellas and one treecreeper). Also most of the forest-dwelling raptors are very rare and infrequently encountered, despite their high

species richness (Beehler *et al.* 1986). Also vultures are absent from New Guinean avifauna (with the gap partly filled by Brahminy or Whistling Kites occurring in open areas across studied sites), again thanks to paucity of large terrestrial vertebrates.

In spite of abundance of expeditions conducted over more than two centuries, there are still birds that are scarcely known in Papua New Guinea, and good-size regions remain ornithologicaly untouched. Most of the available information and species lists date back to 1980's, while ornithological survey slowed down during last decades. Scarce observations come mainly from birdwatchers. Unlike many other ornithological expeditions and surveys in the region, I conducted a standardized and complex survey designed across complete altitudinal gradient (first four studies) and in various habitats in lowland forests (last two studies). I focused on ecology of birds with different feeding specializations, and on ecology of insectivorous birds and their food preferences. This allowed me to describe the food specializations and habitat preferences for previously poorly known birds.

I provided interesting insights into the factors responsible for patterns of species richness. I applied rarely used or novel methods to study food preferences of birds and their predation pressure on herbivores. As such, I provided more detailed information on the shortcoming of the methods and their use in the field. Many more detailed studied on birds communities are not part of the thesis and will be published later. Namely studies on bird community composition, their abundances, and most of the work relaying on body measurements. Besides the direct analyzes and field work, I produced also many educational booklets, and one complete internet database (see Appendices) including information about most of the New Guinean birds. I hope that those will attract interest of wide public and local people, as well as the thesis will serve as a determination or inspiration for future studies on New Guinean birds.

MAIN FINDINGS

The *first chapter* focused on the altitudinal species richness of birds and birds partitioned into feeding guilds and its drivers. I explored the main environmental factors that might influence observed patterns: available area, regional species pool, mid-domain effect, climatic conditions, and habitat characteristics. In agreement with many other studies, I found the species richness to be the highest in lowlands (133 forest bird species) and decreasing towards to the highest altitudes (37 forest bird species at the tree line). Beehler (1986) reported mean of 100 bird species at 1,500 m, 75 from 2,500 m, and 25 species from 3,500 m from various site in New Guinea, and proposed the reduction of available area, decrease in temperature and decrease in tree height and habitat structural diversity as possible explanations. In comparison to

Beehler, I observed more bird species in higher altitudes of Mt. Wilhelm and identified habitat complexity as the main driver of observed patterns for all birds, especially for insectivorous birds. Frugivorous birds followed slightly different pattern of species richness which correlated strongly with climatic conditions. Overall, habitat complexity, climatic conditions and regional species pool received the strongest support as the drivers of altitudinal species richness. On the other hand, area and mid-domain effect were particularly poor predictors of avian species richness and are thus unlikely as mechanisms underlying these species richness patterns.

The focus of *the second chapter* was to describe new range extensions and bird species previously not recorded in the region of Eastern slopes Mt.Wilhelm. Based on the field work conducted in 2010 – 2012 and three expeditions along the altitudinal gradient; I present novel distributional information for 52 bird species. This includes range extensions, demographic data and altitudinal range shifts. I recorded 29 bird species with upwards range shifts compared to previously published literature, and tentatively concluded that upward (but not downward) range extensions and shifts are probably real, rather than resulting from poor quality of previous information. I also provided observed altitudinal ranges of all bird species recorded during standardized survey methods (analyzed in *first chapter*) and few bird species recorded in addition to them, or excluded from analyzes in *first chapter* (i.e. raptors).

In the *third chapter,* I focused in detail on feeding specializations of birds mist-netted along the altitudinal gradient. I employed relatively rarely used method of non-lethal sampling by emetic tartar. I found the method useful and harmless to tested birds. Overall, I forced 999 birds to regurgitate and my data set comprised 99 species occurring at 10 different altitudinal sites. I analyzed 739 food samples from 99 bird species, and identified 3,504 food items (i.e. arthropod individuals, seeds or other plant materials), from which 2,728 items were arthropods. The information of feeding preferences was previously unknown for most of the bird species sampled by us. I was thus able to report and analyze new information about many New Guinean birds. I also clustered species into feeding guilds based on the obtained datasets, which helped us in further analyzes. I also pointed some altitudinal trends in food preferences (i.e. bird taking relatively less arthropods at the highest altitudes than in the lowlands), and correlation between body sizes of birds and food items.

In the *fourth chapter,* I studied predation pressure on an artificial arthropod – a clay caterpillar – along the altitudinal gradient. I focused the study on the two main predators of arthropods in the tropical forest – birds and ants. The method used in this study is relatively new, and seems to be useful for studies comparing predation rate of a given predator between various sites. I used the clay models exposed on leaves with herbivory and on leaves without herbivory to find out whether birds and ants orient themselves according to herbivorous damage while searching for food. I completed the study with survey on abundances of ants and abundances of insectivorous birds occurring in forest interior (as a part of study in *first chapter*). I found that clay caterpillars placed on leaves with mechanical damage are significantly more attractive for both birds and ants. However, the damaged leaves were more attractive for ants than for birds. The majority of all recorded attacks on caterpillars were made by ants (36 % of recorded attacks), and birds (42 %), followed by attacks by unidentified insects, probably mainly by grasshoppers and crickets (4 %), wasps (4 %), and parasitoids (1 %). Along the gradient, the number of attacks by birds correlated with the species richness and abundances of insectivorous birds. The ants caused majority of attacks in lowlands, but their predation decreased with altitude, and we did not find any ants and any ant marks on caterpillars above 2700 m asl On the other hand, bird marks on clay caterpillars were relatively rare at the lowest altitude, and birds only become more important predators at mid altitudes, where ants were already disappearing.

The *fifth chapter* focused on bird communities in forest fragments in lowlands. Lowland bird communities are naturally species rich, but lowland forest in New Guinea is currently endangered by logging activities, and fragmented at a rapid rate. I therefore focused on the effect of fragmentation of bird communities. I found that none of the studied forest fragments housed the same number of species as continuous forest. However, forest fragments of 300, 600 and 1200 ha housed still more than 80% of bird species recorded in primary continuous forest, and the difference between species richness in fragments was not significant. I further identified the most sensitive bird species between frugivores and insectivores, and their habitat preferences. I also used non-lethal emetic tartar method (same as in the *third chapter*) to survey food taken by six species mist-netted in all fragments, and completed the study by arthropod sampling. I concluded that food availability doesn’t seem to limit insectivorous birds in studied fragments. Also microclimate in forest fragments did not differ significantly from the continuous forest, and was unlikely to influence birds negatively. More importantly, I found that the sensitive bird species (e.g *Monarchidae*, *Rhipiduridae* and *Acanthizidae*) foraged preferably in microhabitats that differed from those broadly available in forest fragments, and were rare in forest fragments. I concluded that microhabitat influenced insectivorous birds, and that forest structure (especially litter cover, canopy openness, and foliage structure) plays important role in shaping bird communities.

In the *sixth chapter*, I again studied attacks on artificial caterpillars, recorded in four habitats: primary forest, secondary forest, forest fragment in lowlands (200 m asl), and montane primary forest (1700 m asl). I compared incidence of attacks of different natural enemies on semi-concealed and exposed caterpillars. I aimed to find out whether leaf rolls, folds and ties protect caterpillars from predators, particularly birds, ants and wasps or whether they serve as cues to predators and thus have negative effects on survival. We exposed a total of 14 400 caterpillars, and identified 2443 attack attempts. The exposed caterpillars were predated significantly more than the caterpillars in leaf rolls. The study shows that human disturbance can affect the biotic interactions between caterpillars and predators. Similarly to the results in fourth chapter, I show here than birds are relatively more important predators at higher altitudes, and that birds are compensating for ant disappearance.

In summary, the results of the thesis demonstrated high sensitivity of insectivorous birds to habitat characteristics, thus their sensitivity to changes in habitat structure. I show that insectivorous birds are likely to be limited by presence of suitable microhabitats (both in lowlands and along altitudinal gradient) and forest strata complexity. Insectivorous birds then tend to disappear from disturbed habitats (or do not inhabit less complex forest), which results in dramatic changes in trophic interactions with arthropods, representing their food resources. I also showed that arthropods are limited by different kinds of predators in different habitats and at different altitudes.

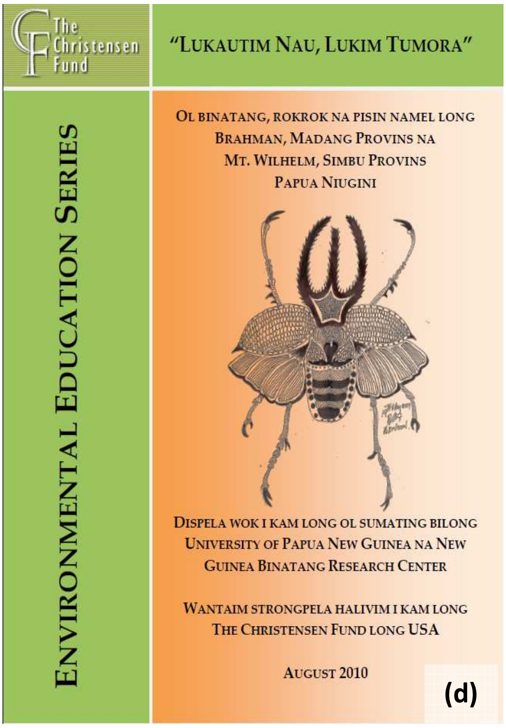
Reference:

Beehler, B. M., T. K. Pratt, and D. A. Zimmerman. 1986. Birds of New Guinea. Princeton University Press.

APPENDICES

Appendix 1. An example of work with local assistants and their traditional knowledge about birds, which helped me a lot during my field work. I was working with villagers speaking eight local languages, recording local names of all birds in their languages. The table presents an example of vernacular names in three languages for five bird species. Figures shows (a) men from Sinopass (2200 m asl), (b) men mist-netting birds in Bruno Sawmill (2700 m asl, (c) school children interested in knowledge of their village leader, (d) front page of the education booklet made for schools along altitudinal gradient, showing diversity of insect ("binatang") frogs ("rokrok") and birds ("pisin").

Bird species	Biyom	Gende	Kuman
Lichenostomus sp.	nafena	togi	tynarengoro
Melidectes fuscus		gori zoro	minmogoyagl
Melipotes fumigatus		gori toro	wocha
Melidectes belfordi		mori	auka (Juv.)9
			mucha (Ad.)
Melidectes princeps	X	kwakija	paunangojach



"Lukautim Nau, Lukim Tumora"

Environmental Education Series

Ol binatang, rokrok na pisin namel long
Brahman, Madang Provins na
Mt. Wilhelm, Simbu Provins
Papua Niugini

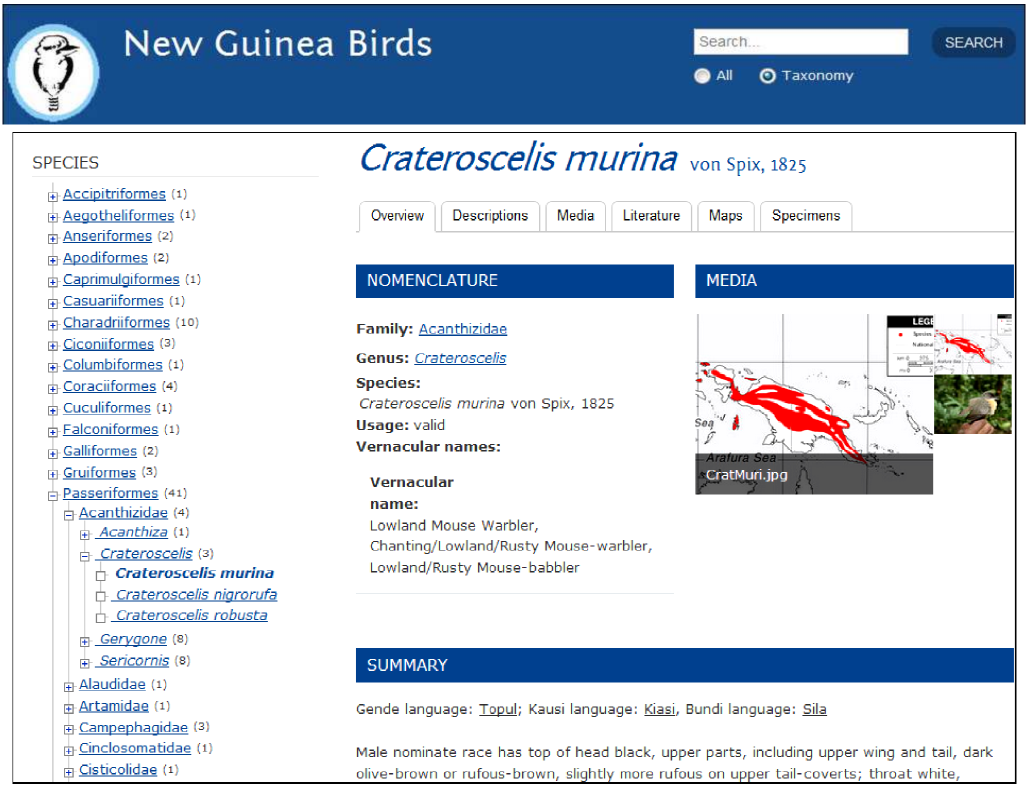
Dispela wok i kam long ol sumating bilong
University of Papua New Guinea na New
Guinea Binatang Research Center

Wantaim strongpela halivim i kam long
The Christensen Fund long USA

August 2010

Appendix 2. An example of bird species description published on web encyclopedia of New Guinea birds which I developed during my Ph.D. study. Encyclopedia includes descriptions, maps, sounds, photos of most of the species occurring in the region.

http://pngbirds.myspecies.info/



New Guinea Birds

Search... SEARCH

○ All ● Taxonomy

SPECIES

- Accipitriformes (1)
- Aegotheliformes (1)
- Anseriformes (2)
- Apodiformes (2)
- Caprimulgiformes (1)
- Casuariiformes (1)
- Charadriiformes (10)
- Ciconiiformes (3)
- Columbiformes (1)
- Coraciiformes (4)
- Cuculiformes (1)
- Falconiformes (1)
- Galliformes (2)
- Gruiformes (3)
- Passeriformes (41)
  - Acanthizidae (4)
    - *Acanthiza* (1)
    - *Crateroscelis* (3)
      - ***Crateroscelis murina***
      - *Crateroscelis nigrorufa*
      - *Crateroscelis robusta*
    - *Gerygone* (8)
    - *Sericornis* (8)
  - Alaudidae (1)
  - Artamidae (1)
  - Campephagidae (3)
  - Cinclosomatidae (1)
  - Cisticolidae (1)

Crateroscelis murina von Spix, 1825

Overview | Descriptions | Media | Literature | Maps | Specimens

NOMENCLATURE

Family: Acanthizidae

Genus: *Crateroscelis*

Species:
Crateroscelis murina von Spix, 1825
Usage: valid
Vernacular names:

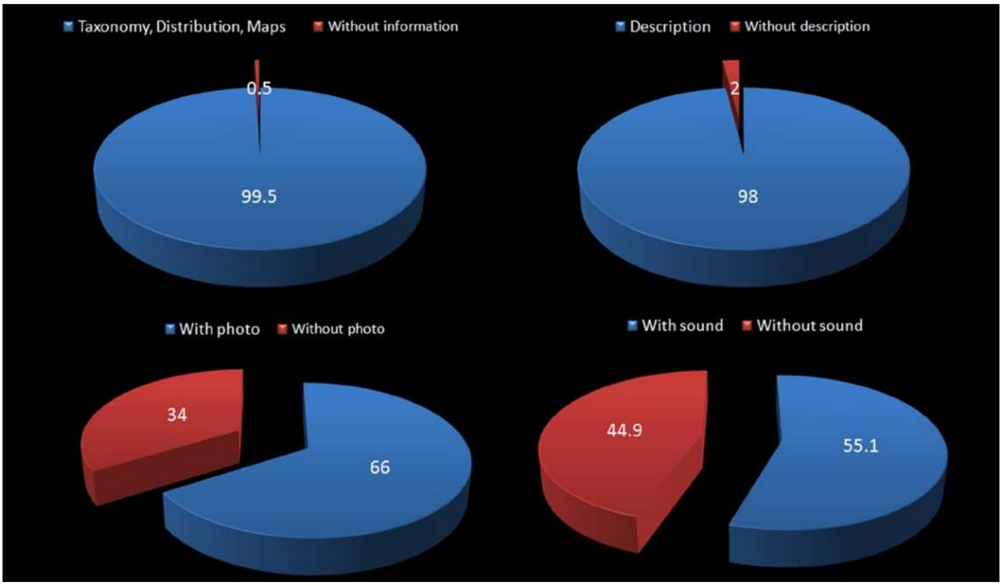
Vernacular name:
Lowland Mouse Warbler,
Chanting/Lowland/Rusty Mouse-warbler,
Lowland/Rusty Mouse-babbler

MEDIA

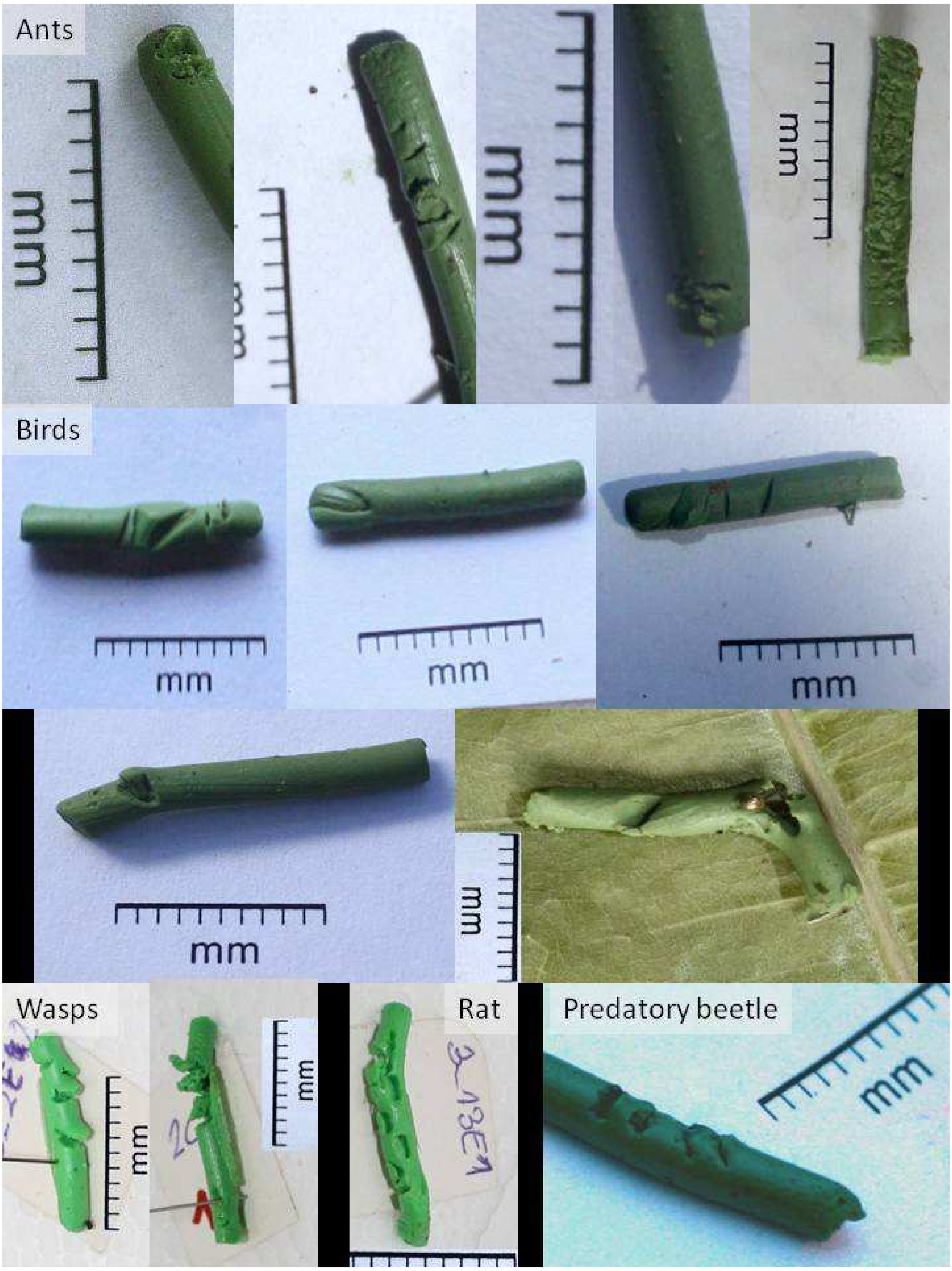
SUMMARY

Gende language: Topul; Kausi language: Kiasi, Bundi language: Sila

Male nominate race has top of head black, upper parts, including upper wing and tail, dark olive-brown or rufous-brown, slightly more rufous on upper tail-coverts; throat white,



Appendix 3. Examples of attack marks made by natural predators of caterpillars. Full guide available online: http://tvardikova.weebly.com/downloads.html



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